HABITAT ASSOCIATIONS OF CAVITY-NESTING OWLS IN THE SIERRA NEVADA

A Thesis

by

JULIE ELIZABETH GROCE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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ABSTRACT

Habitat Associations of Cavity-Nesting Owls in the Sierra Nevada. (August 2008)

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Chair of Advisory Committee: Dr. Michael L. Morrison

Several species of small, cavity-nesting owls occur in the Sierra Nevada, including in areas impacted by human activities. The owls typically use standing dead trees (snags) for nest sites. Although descriptive studies exist regarding habitats associations around nest and roost sites, few studies have examined habitat associations at larger spatial scales or relative to certain snag characteristics (e.g., density, decay class). To improve our understanding of the habitat associations of these owls, I compared habitat characteristics at 2 spatial scales around areas of owl detection and non-detection. I also examined distances between conspecifics and heterospecifics to determine if clustering of conspecifics or avoidance of predators occurred. I conducted owl broadcast surveys and snag sampling during the spring and summer of 2006 and 2007 in the Lake Tahoe Basin of central Sierra Nevada. I measured additional habitat variables (e.g., vegetation cover, distance to roadways) from pre-existing geographical information system layers. I used stepwise logistic regression to ascertain which variables were influential in predicting owl occurrence. The northern saw-whet owl (*Aegolius acadicus*) was the only species detected in sufficient numbers for statistical analysis, with a detection probability of 0.25. I detected saw-whets in a wide range of conditions and it appeared

that few factors influenced their distribution in the basin. Areas dominated by white fir, however, were correlated with the absence of saw-whets at both the macrohabitat and microhabitat scales. White fir-dominated areas tend to occur on the west side of the basin and it is possible white fir was acting as a proxy for other factors not measured in this study, such as microclimate conditions or prey availability. I was also more likely to find a saw-whet within 1000 m of another saw-whet than within 1000 m of a non-use point, indicating clustering of conspecifics in the basin. While it appears saw-whet needs are being met in the basin, restoration projects are ongoing to decrease both the number of snags and relative abundance of white fir. Continued monitoring of the species is essential to understand potential effects of restoration activities. Suggestions are provided for appropriate timing and effort of future surveys.

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INTRODUCTION

The impacts of human activities on forest-dwelling wildlife populations in the United States have been the focus of numerous studies over the past several decades (e.g., USFS 2008). In the Sierra Nevada of California, human impacts have included logging, livestock grazing, development, recreation, and fire suppression, resulting in the alteration of the vegetation composition and structure of many forest stands (Beesley 1996, Manley et al. 2000). Owls comprise a large portion of the top avian predators in the region and the potential effects of human activities on owl populations are not well understood (e.g., Johnsgard 2002). To understand how past, present, or future human activities and forest management practices might influence the distribution of owls, we must begin with a thorough examination of their habitat associations. Here I discuss habitat associations of small, cavity-nesting owl species in a region of the Sierra Nevada with a long history of human impacts.

Seven species of owls are known to occur in higher elevations (>1800 m) of the central Sierra Nevada: flammulated owl (*Otus flammeolus*), northern pygmy-owl (*Glaucidium californicum*), northern saw-whet owl (*Aegolius acadicus*), western screech-owl (*O. kennicottii*), long-eared owl (*Asio otus*), great horned owl (*Bubo virginianus*), and California spotted owl (*Strix occidentalis occidentalis*) (Orr and Moffitt 1971, Schlesinger and Romsos 2000). Researchers have conducted multi-

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species owl surveys in recent years in selected areas (Manley et al. 2002, Roth et al. 2004), yet studies of habitat associations in the region have focused primarily on the California spotted owl (e.g., Bias and Gutierrez 1992, Seamans 2001, Bond et al. 2004). Most information on other owl species in the area is from naturalists' descriptions in the early to mid-1900s (Grinnell and Miller 1944, Orr and Moffitt 1971) or from incidental detections (Crozier et al. 2003). To supplement existing information, I examined habitat characteristics around detections of the small (<200 g) cavity-nesting species – the flammulated owl, northern pygmy-owl, and northern saw-whet owl – to better understand the habitat associations of these cavity-dependent species and determine any potential limiting factors. Although the western screech-owl is also considered a small, cavity-nesting owl, the species' apparent rarity in certain areas of the central Sierra Nevada precluded them from this study.

Throughout the text, *habitat* refers to an area containing a combination of resources and environmental conditions that promote occupancy, survival, and reproduction by individuals of a species (Morrison et al. 2006:10). Habitat includes both abiotic and biotic factors, from precipitation rates to the presence of predators or competitors. The existence of particular combinations of abiotic and biotic conditions is the result of complex interactions of functions and processes occurring at multiple spatial and temporal scales (Levin 1992, Corsi et al. 2000). Examining a species' habitat at a range of scales is necessary for a comprehensive understanding of the species' needs, from the macrohabitat (corresponding to the distribution and abundance of populations) to the microhabitat (corresponding to the needs of an individual) (Block

and Brennan 1993:38). In this study, I examined features at broad (macrohabitat) and fine (microhabitat) spatial scales to describe several habitat characteristics of the small, cavity-nesting owls. I inferred the presence of the owls indicated use of an area; that is, the individuals were using resources to meet survival needs (e.g., foraging, nesting) (Block and Brennan 1993:38).

Correlating the presence or abundance of a species to measureable habitat variables allows for the creation of models to asses or predict species occurrence (e.g., Scott et al. 2002). Previous studies indicated several habitat variables as potentially informative in predicting occurrences of flammulated, northern pygmy, and northern saw-whet owls. At the macrohabitat scale, habitat variables included elevation (Grinnell and Miller 1944, Winter 1974, Cannings 1993, Johnsgard 2002), vegetation classes (e.g., open canopy forest) (Johnsgard 2002, CWHR 2000), and extent of canopy cover (Goggans 1986, Christie and van Woudenberg 1997). The small owls typically occur in mixed and montane conifer forests with scattered forest openings in which to forage (Johnsgard 2002). While useful on a broad geographic scale (e.g., state-wide), this information is so general as to be virtually uninformative at finer scales (Wiens 1989, Mitchell et al. 2001). For example, the California Wildlife Habitat Relationship System (CWHR 2000) indicates that the small owls range throughout the Lake Tahoe Basin in California, yet surveys in recent years suggest large gaps of occurrence in the basin (K. L. Borgmann and M. L. Morrison, unpublished report to U.S. Forest Service). On the other extreme, results of studies on microhabitat features showed varying degrees of owl association with particular tree species (Cannings 1993, Holt and Petersen 2000,

Johnsgard 2002). Due to the site-specific nature of the studies, not all findings are in agreement and extrapolation to other areas is tenuous (Wiens 1989). Studies that incorporate habitat associations at multiple spatial scales may better serve our understanding of a species' needs.

The majority of studies dealt with microhabitat variables (i.e., at or near nest or roost site), and indicated that presence of large trees or snags (Marcot and Hill 1980, Hayward and Garton 1988, Bull et al. 1990a, Cannings 1993, Johnsgard 2002, Giese and Forsman 2003), presence of quaking aspen (*Populus tremuloides*) (Palmer 1986, Smith 1991, Anderson and Clark 2002), distance to forest openings (Cannings 1993, van Woudenberg 1999, Anderson and Clark 2002), and distance to riparian areas (Palmer 1986, Hayward and Garton 1988) may aid in predicting occurrence. Several studies also noted the use of forest edge or forest openings by the owls for hunting (Forbes and Warner 1974, Cannings 1993, McCallum 1994), although the extent of edge use remains debatable (e.g., Giese and Forsman 2003).

Regardless of the tree species, the presence of cavities is an essential component for the small owls. Flammulated owls, northern pygmy-owls, and northern saw-whet owls are secondary cavity nesters, typically nesting in naturally formed tree cavities or, more often, cavities excavated by other avian species (Scott et al. 1977, Bull 1997). Cavities created by northern flickers (*Colaptes auratus*), pileated woodpeckers (*Dryocopus pileatus*), and sapsuckers (*Sphyrapicus* spp.) are most commonly used in many parts of the owls' ranges (Bull et al. 1990a, Arsenault 1999); hairy woodpeckers (*Picoides villosus*) are also an important excavator in the central Sierra Nevada (Raphael

and White 1984). These primary excavators often create cavities in standing dead trees, known as snags. Although researchers acknowledge snags as an important component of the owls' habitat, few studies have examined the relationship between snag characteristics (e.g., density, size) and owl presence at scales greater than that of the immediate nest area (Johnson and Anderson 2003).

While vegetation and other physical features have a role in defining owl distributions, the presence of conspecifics or heterospecifics may also be influential. For example, large owls (e.g., long-eared owl, great horned owl, California spotted owl) are known predators of the small, cavity-nesting owls (Voous 1989, Johnsgard 2002) and may limit the presence of small owls in areas that otherwise appear habitable (Cody 1985). In addition, clustering of conspecifics is known to occur in certain owl species, although the reasoning as to why remains speculative (Arsenault 1999, Seamans and Gutierrez 2006). Overlooking or ignoring the possible influences of the presence of one owl on another may inhibit the predictive capabilities of distribution models (Campomizzi et al. 2008). Few studies of small owls, however, have attempted to quantify and incorporate sociality into their distribution models.

Defining the owls' habitat associations at multiple spatial scales, along with including sociality components, can lead to an increased understanding of potentially limiting factors along with providing recommendations for creating and maintaining appropriate habitat. My goal was to increase understanding of small, cavity-nesting owls in the central Sierra Nevada by examining their distributions and habitat associations at both a broad and fine scale. Within this goal, my first objective was to

document their distributions based on nocturnal broadcast auditory surveys and determine the detection probabilities for each species. Quantifying detection probabilities was necessary to ascertain whether owls were actually absent from an area or simply not detected. The validity of the results depended in part on these probabilities. If individuals are undetected, and thus presumed absent when they are in fact present, all subsequent analyses of habitat use versus non-use are in jeopardy (MacKenzie et al. 2006:11). In addition, knowing the detection probabilities would help to establish the minimum survey effort needed to determine absence of an individual in future surveys (MacKenzie and Royle 2005). My second objective was to examine the relationship between habitat characteristics and owl occurrence at both broad (i.e., macrohabitat, averaging about 260 ha) and fine (i.e., microhabitat, about 20 ha) scales. The microhabitat scale of 20 ha was roughly the size of the estimated core area of the owls' territories (Johnsgard 2002) while the macrohabitat scale was large enough to potentially encompass several individuals. For macrohabitat, I examined patterns of vegetation cover, including edge density, and proportions of dominant tree species. Edge density is a measure of the length of edge per unit area, indicating the extent of interface between 2 or more different habitats (McGarigal and Marks 1995:89). For microhabitat, I examined vegetation cover, snag characteristics, and distances to select habitat features indicated in the literature to be important. Lastly, by identifying habitat characteristics at both scales that relate to small, cavity-nesting owl occurrence, my final objective was to provide useful information for future monitoring and management of some of the biotic resources in the central Sierra Nevada.

STUDY AREA

My study area was the Lake Tahoe Basin (LTB), which straddles the border of California and Nevada on the eastern side of the Sierra Nevada (Fig. 1). It covers approximately 1,300 km^2 (131,100 ha), nearly 500 km^2 of which is the lake itself, with elevations of 1,900 m at the lake surface to 3,315 m (Elliott-Fisk et al. 1997). Daily average temperatures range from -7.2 to 25.5°C throughout the year (Western Regional Climate Center [WRCC] 2007). Nightly temperatures during nocturnal surveys in May–July 2006 ranged from -2.5 to 20.0°C ; temperatures ranged from -10.0 to 14.0°C during nocturnal surveys in March–June 2007. Average annual precipitation is 81 cm with the majority falling between December and March as snow, although precipitation tends to decline along a west-to-east gradient (Manley et al. 2000, WRCC 2007). Total precipitation during the 2006–2007 field seasons was below average: 1.37 cm for May–July 2006 and 8.64 cm for March–June 2007, versus a long-term (90-year) average of 5.33 cm for May–July and 20.47 cm for March–June (WRCC 2007).

The LTB has changed considerably in the past 150 years due to human activity. Beginning in the mid-1800s, small-scale logging occurred throughout the LTB while large-scale logging occurred primarily in the northern, eastern, and southern areas. By 1900, 60% of the LTB was clearcut (Lindström 2000). Small-scale logging continues today in the form of fuel reductions by the U.S. Forest Service. Cattle and sheep grazing was heavy from 1900 until the 1930s at which time restrictions were implemented (Lindström 2000). Development and tourism have grown exponentially in the last

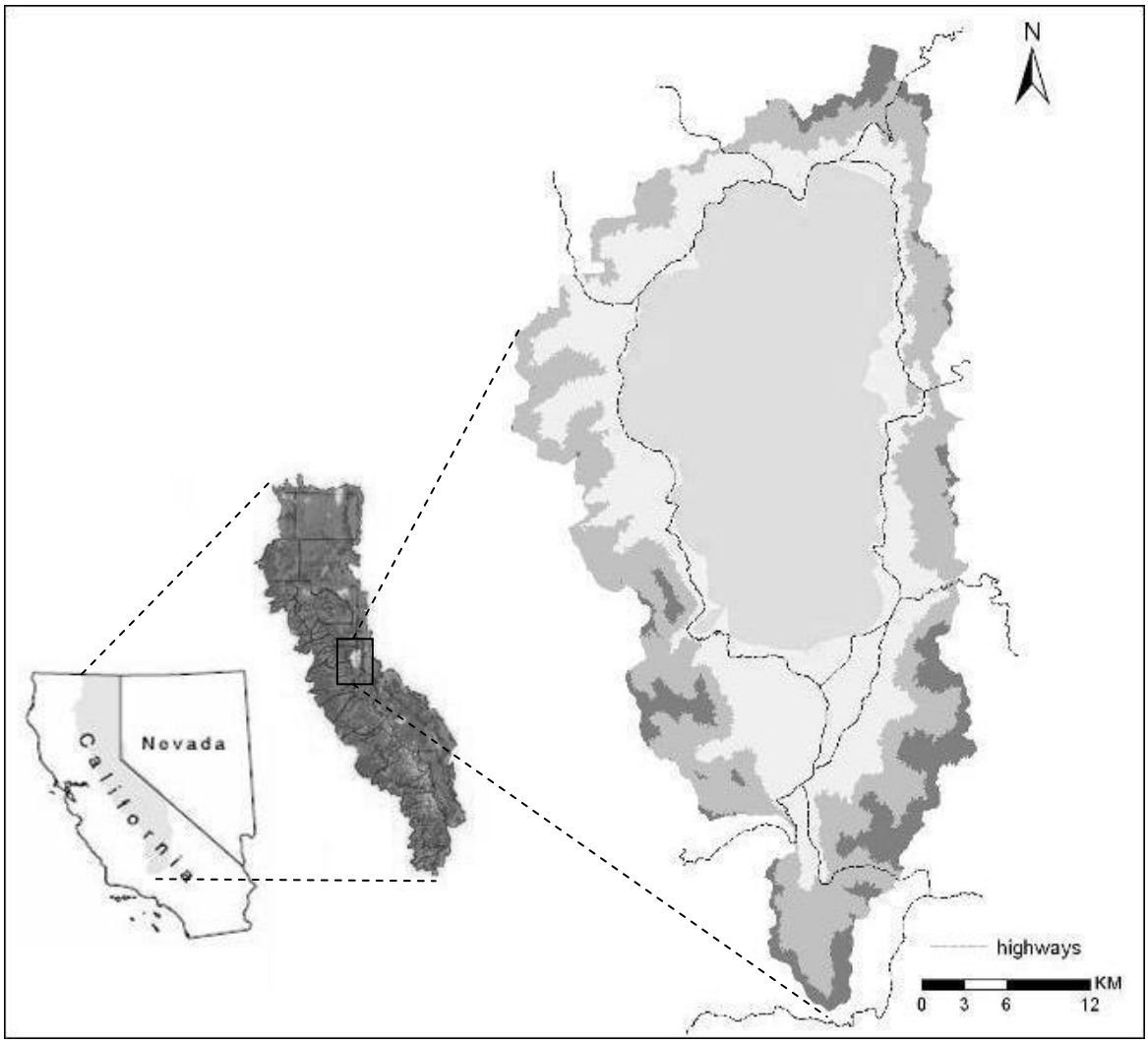

Figure 1. Map of the Lake Tahoe Basin relative to the Sierra Nevada and the states of California and Nevada. Shaded areas of the basin indicate 3 elevation ranges: <2,200 m, 2,200–2,600 m, and >2,600 m, with the lightest shade corresponding to the lowest elevations.

century; the LTB is home to over 60,000 permanent residents and sees an estimated 23 million tourists annually (Elliott-Fisk et al. 1997). Approximately 1,700 km of state highways, national forest roads, and private roads, along with hundreds of kilometers of hiking trails, extend throughout the LTB and make most of the forest relatively accessible to human use. The U.S. Forest Service Lake Tahoe Basin Management Unit (LTBMU) currently manages 80% of the land in the LTB (LTBMU 2008).

Manley et al. (2000:409–412) described 3 main vegetation zones in the LTB. The lower montane zone (<2,200 m) is comprised mainly of Jeffrey pine (*Pinus jeffreyi*) forests, white fir (*Abies concolor*) forests, and mixed conifer forests (i.e., white fir, Jeffrey pine, and lodgepole pine [*P. contorta*] with lower densities of sugar pine [*P. lambertiana*] and incense cedar [*Calocedrus decurrens*]). The upper montane zone (2,200–2,600 m) contains forest types dominated by red fir (*A. magnifica*), with lodgepole pine in wet areas, and it has less shrub and herbaceous cover than lower elevations. The subalpine zone (>2,600 m) contains mainly a mixed subalpine woodland of mountain hemlock (*Tsuga mertensiana*), whitebark pine (*P. albicaulis*) and smaller proportions of red fir, lodgepole pine, and western white pine (*P. monticola*). Wet and dry meadows, quaking aspen groves, and riparian areas are scattered throughout the LTB.

Due primarily to logging in the 1800s and fire suppression in the last century, the forests now typically contain higher tree densities and smaller trees than previously (Manley et al. 2000, Taylor 2007). Dense stands of white fir has been attributed, in part, to fire suppression (Parker 1984). Tree species composition has shifted from mostly

pine and other fire-tolerant species to fire-intolerant firs. The relative abundance of Jeffrey pine, for example, has declined by about half, whereas the relative abundance of white fir has doubled (Manley et al. 2000:428). In addition, researchers from the University of California, Davis, estimate that 20–25% of the trees in the LTB are dead or dying, due primarily to drought and insect infestation from 1988 to 1992 (Rizzo and Maloney 2000).

METHODS

Survey site selection

Prior to my study, several owl surveys had occurred in scattered areas of the LTB and surrounding forests (Manley et al. 2002, Roth et al. 2004), including 2 seasons (May–August 2004 and 2005) of surveys within certain watersheds on the California side of the LTB (K. L. Borgmann and M. L. Morrison, unpublished report to U.S. Forest Service). LTBMU restoration projects were intended for these areas and multi-species inventory and monitoring were underway to provide pre-restoration baseline data. Surveys entailed broadcasting owl calls from specified points (hereafter referred to as call points). Due to the specific restoration needs and intentions, these areas of LTBMU interest had not been selected probabilistically; the starting location for the first call point within each site, however, had been randomly located. Since the owl surveys were part of the larger LTBMU monitoring program, I retained the call point locations for my study with slight modifications in the spacing or number of points. Thus, in 2006, I established 96 call points in 14 groups, with each group covering an area of interest to the LTBMU. Most groups contained 7–8 call points (range of 2–8 call points) with each point spaced 500 m apart to allow for adequate cover of the areas of interest and spatial independence of the points (Morrison et al. 2008:202, Johnsgard 2002). I added 36 new call points in 5 groups (5–9 call points per group) in a systematic fashion: I added a new group of call points outside of, but adjacent to, every third LTBMU area with the first area randomly chosen (Fig. 2).

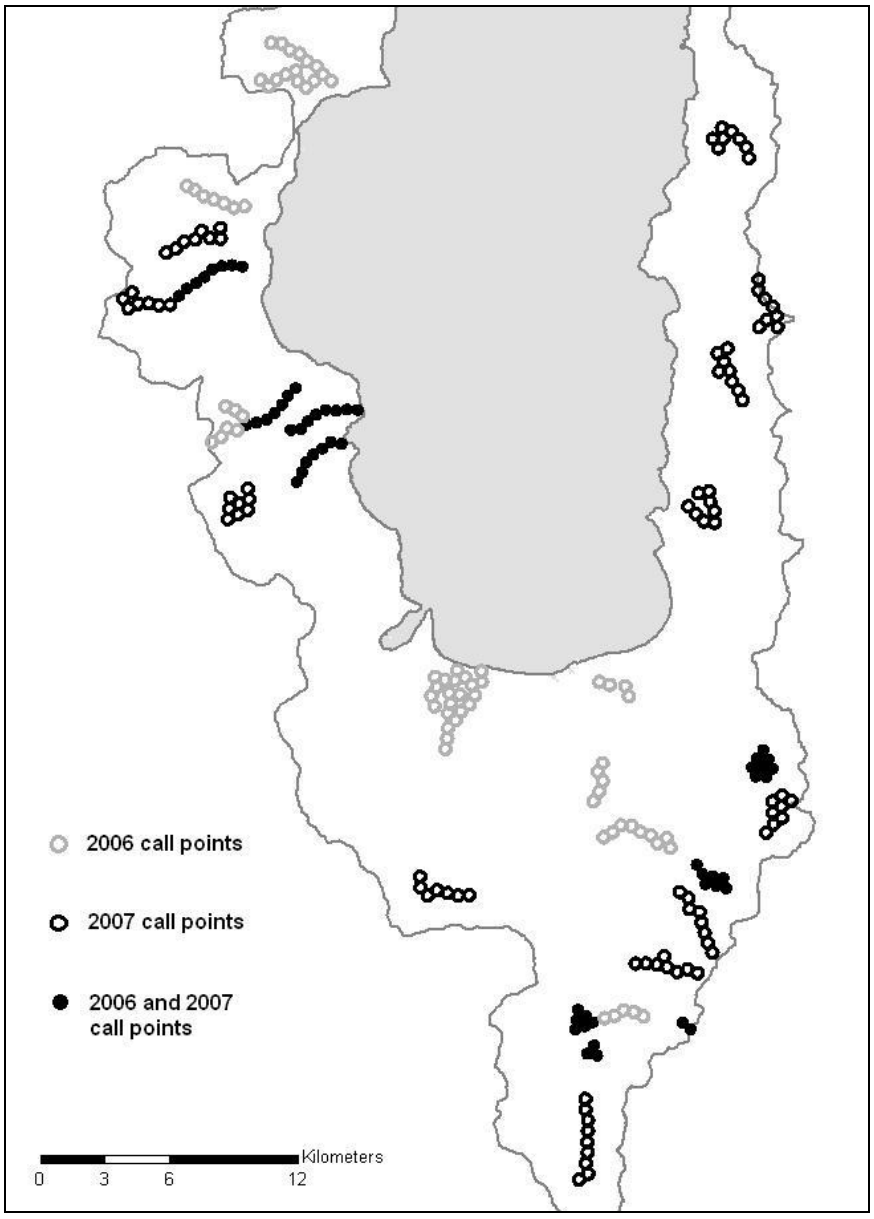

Figure 2. Area covered by owl broadcast surveys at call point locations during May–July 2006 and March–June 2007 in the Lake Tahoe Basin, California and Nevada. Circles indicate 250 m effective call radius.

In 2007, I surveyed 150 points throughout the LTB, 56 of which were the same points as in 2006 (i.e., LTBMU areas of interest) (Fig. 2). The 94 new call points were combined into 12 groups (7–9 call points per group, each point spaced 500 m apart). I walked between call points to allow for hearing owls en route and group placement of call points facilitated efficiency and allowed me to survey a greater number of call points each night. I determined the placement of each group by employing a stratified random sampling scheme based on elevation and dominant vegetation cover type (as defined by Dobrowski et al. 2005). Thus, I stratified call points within 3 elevation categories (<2,200 m, 2,200–2,600 m, and >2,600 m) and avoided large areas of shrub-dominated or non-vegetated areas where the small, cavity-nesting owls would not typically occur. Most of the LTBMU areas of interest were in the lower elevation category; therefore, the majority of the new 2007 call points were in the mid and high elevations (Fig. 2).

To determine exact locations of the call points, I first used ArcMAP and a geographic information system (GIS) vegetation layer (Dobrowski et al. 2005) to establish random points in areas >2,200 m and of open or closed canopy. I placed a 900-m buffer around each random point, as that size encompassed roughly the amount of area covered by 8 call points spaced 500 m apart. I then deleted all buffered locations that (1) overlapped with existing LTBMU call points, (2) were outside U.S. Forest Service land boundaries, (3) were further than a 2-hour hike from a drivable road, and (4) contained sufficiently steep slopes that would jeopardize the safety of the surveyors. Further, I did not include the far northern section of the LTB when selecting call point locations because access to those areas was logistically infeasible. I randomly selected

from the remaining buffers in proportion to the amount of land area contained within each elevation category.

I placed call points within the aforementioned 900 m buffers by first inserting a random point on ArcMAP within the buffer. All other call points within the buffer were placed relative to this first point and based on (1) maintaining 500 m spacing, and (2) topography (e.g., avoiding sections of notably steep, unsafe slopes). Once established in ArcMAP, the points were then ground-truthed which resulted in slight shifting of the call points due to reality of the terrain and GPS satellite reception. Although some call points did end up on roads, the roads were small, unpaved, and infrequently used by motorized vehicles. Most roads were indiscernible from the surrounding landscape when snow covered the ground (i.e., the roads created minimal, if any, gaps in the canopy cover). Some call points were also along hiking trails but the trails likewise created minimal disturbance in the surrounding vegetation.

I allocated the number of call points in proportion to the amount of land covered by each category; thus, elevations of <2,200 m had the highest number of call points while elevations >2,600 m had the fewest call points. High elevation options occurred primarily in the southeastern section of the LTB.

Broadcast surveys

Nocturnal broadcast surveys consisted of projecting owl calls through an amplified speaker to induce an owl in the vicinity to respond. Numerous studies have shown this type of survey to be effective when dealing with cryptic or nocturnal species (e.g., Johnson et al. 1981, Bosakowski and Smith 1998). Surveys occurred with 1–2

observers. In 2006, we surveyed the sites from May to July. In 2007, we conducted broadcast surveys from mid-March to June. March is typically the onset of the breeding season for many owl species, a time of courtship displays and territorial behavior (Johnsgard 2002). By initiating surveys in March, we anticipated an increase the number of owl detections (Palmer 1987, Clark and Anderson 1997, Crozier et al. 2003).

We broadcasted the calls of 6 owl species using a portable CD player and Foxpro Wildlife Caller® in the order of smallest to largest species (i.e., flammulated owl, northern pygmy-owl, northern saw-whet owl, western screech-owl, long-eared owl, and great horned owl). Although broadcasting the calls of larger-bodied owls does not always deter smaller owls from responding (Boal and Bibles 2001, Manley et al. 2002:118, personal observation), researchers have recommended that multi-species broadcasts should be arranged from smallest to largest species to avoid possible intimidation of the smaller species (Fuller and Mosher 1981, Hayward and Garton 1988). We included long-eared owl and great horned owl calls so as to document the locations of these potential predators. Because the LTBMU maintains a separate project focused on California spotted owls, we did not include this species in the surveys. We set the volume of the broadcasting unit such that it was barely audible to the surveyor at a distance of 250 m; thus, each call point effectively covered approximately 20 ha. We used standard owl calls taken from Peterson Field Guides® and Stokes Field Guide to Bird Songs®. Each broadcast session began with 5 minutes of listening. We then broadcasted each species for 30 seconds followed by 30 seconds of silence and repeated each species twice in succession. We listened for an additional 5 minutes at the end of

the broadcast series. Thus, we remained at each call point for 22 minutes. For each owl detected, we recorded the species and the direction and distance of its response. Distances were estimated and categorized: 0–10 m, >10–50 m, >50–100 m, >100–200 m, and >200 m. When possible, we triangulated on the owl to increase the accuracy of its estimated location or located the tree from which the owl called.

To coincide with typical peak activity periods (Johnsgard 2002), we began each survey 15 minutes after sunset and continued until completion of all call points in a series (usually between midnight and 0200). Initiating the evening surveys soon after sunset potentially increased the chances of detecting the diurnal northern pygmy-owl. We also occasionally surveyed in the few hours before sunrise, following evenings in which we did not complete a group of call point. We changed the order of the call points with each visit to limit the effects of temporal bias (Morrison et al. 2008:211). We did not survey during heavy rain, wet snow, or in winds >20 km/h.

Detection probability

We surveyed each call point either 3 or 6 times. These numbers were determined, in part, by utilizing an equation by MacKenzie and Royle (2005:1109). The equation calculates the appropriate number of points and number of times to survey so as to minimize the possibility of not detecting an individual when it is, in fact, in the area. It incorporates pre-defined estimates of the probability of occupancy and the probability of detection for the species of interest:

$$s = [w/\mathrm{Var}(\hat{w})]\,[(1 - w) + (1 - p^*)/[p^* - Kp(1 - p)^{K-1}]],$$

where w = probability of occupancy, p = probability of detection, $p^* = 1-(1-p)^K$ = the probability of detecting the species at least once, K = number of survey occasions (a value I acquired from Table 1 of MacKenzie and Royle [2005:1110]), and s = number of points to survey. Assumptions when using this equation were (1) the detection probability was constant over time, (2) the outcome of 1 survey did not depend on the outcome of another in space or time (i.e., the call points were independent), and (3) the probabilities for each owl species were the same. I estimated the probabilities for the 2006 surveys based on information available in the literature, which was sparse with regards to owl detection probabilities. I used estimates of 0.2 for probability of occupancy, 0.3 for probability of detection, and a desired standard error of 0.1. These values resulted in the need for 6 surveys at ~20 points throughout the basin. I used a larger number of call points than suggested by the equation so as to provide a cushion for a range of possible probabilities. Any group of call points in which we detected an owl in the first visit was surveyed a total of 6 times, with the justification that the known occurrence of individuals in these areas would aid in calculating detection probability. The apparent rarity of the owls, however, warranted surveying a greater number of call points fewer (i.e., 3) times (MacKenzie et al. 2006:179) so as to cover a larger area and get a clearer understanding of the owls' distributions in the LTB. Thus, we surveyed 77 points 6 times and surveyed 55 points 3 times in 2006.

Results from the May–July 2006 field season indicated low detection probabilities (~0.03–0.07, see Results) for northern saw-whet owls, of which we detected 15 individuals. The value was lower than anticipated, but may have been due to

suboptimal timing of surveys (i.e., surveying too late in the season). Although low detection probability would usually warrant an increase in the number of visits to each call point (MacKenzie and Royle 2005), I decided to continue surveying either 3 or 6 times per point in 2007 because (1) the timing of the surveys in 2007 was more favorable for owl detection, and (2) the amount of hetero- and conspecific broadcasts from more than 6 surveys at a site within a 3-month period could potentially alter the owl's territorial behavior or disrupt its breeding behavior (Johnson et al. 1981). Thus, in 2007, we surveyed 92 points 3 times and surveyed 58 points 6 times. Again, the choice of which points to survey 6 times depended on which areas owls were detected during the first visit, to aid in calculating detection probability.

Analysis.—Due to extremely low detections of flammulated and northern pygmy-owls, I calculated detection probabilities only for northern saw-whet owls (hereafter referred to as saw-whets). I used the program PRESENCE 2.0 (PRESENCE 2006) to calculate detection probabilities for the 3-survey and 6-survey occasions. Because surveys occurred at different time periods in 2006 and 2007, I calculated separate detection probabilities for each year. When calculating detection probabilities for the 3-survey occasions, I also included data of every other survey from call points where 6 surveys occurred (i.e., survey occasions 1, 3, and 5). If I detected the same owl at more than 1 call point during a survey (i.e., a violation of the assumption of spatial independence), I removed 1 of the 2 call points from the dataset prior to analysis. In addition, because many call points were at higher elevations in 2007 than in 2006, I calculated separate detection probabilities for the call points surveyed in both years to

determine whether differences in detection probabilities across years was due to either spatial or temporal factors.

Macrohabitat

Using ArcMAP, I plotted all owl detections based on survey information of distance to and direction from the call points. Due to limited detections of flammulated and northern pygmy-owl detections, I conducted this analysis only for saw-whet owls. I combined owl locations for both years; I did not, however, include owls detected in 2007 that were within 500 m of the same species detected in 2006 due to the potential of the owl being the same individual both years. I acquired GIS layers from USGS (http://tahoe.usgs.gov/) and LTBMU to analyze habitat variables. The layer from the USGS was a 10-m digital elevation model. Layers from the LTBMU included highways, Forest Service roads, local roads, trails, and waterways (all based on IKONOS imagery with 4-m accuracy), and contour lines (12-m intervals). I also acquired from LTBMU a vector format vegetation layer produced by Dobrowski et al. (2005) specifically for the LTB. The vegetation layer consisted of thousands of polygons, each containing a particular combination of vegetation characteristics. The layer was also based on IKONOS imagery, collected in July 2002 (see Greenberg et al. 2005 for details). The authors assessed and validated the accuracy of the data set (Dobrowski et al. 2005, Greenberg et al. 2006). The vegetation map contained information regarding vegetation cover at the class and species level. Vegetation types at the class level included: closed canopy (>60% tree cover), open canopy (0–60% tree cover, although primarily >25% cover), shrubland (shrub-dominated, <25% tree cover),

herbaceous (herb-dominated, <25% tree cover, although primarily <10% tree cover), sparse vegetation (<5% tree cover, although primarily <1% tree cover), and non-vegetated. Species-level classification was based on the dominant species in each polygon and was only possible for the tree and shrub classes.

Using ArcMAP, I created 500 m radius buffers around each call point and combined the area covered by the buffers into a single site to define the macrohabitat. I combined either half or all call point buffers in a group into a single site depending on owl locations. For example, if 2 saw-whets were detected on either end of a group of call points, I combined the entire group into 1 owl-use site; if, however, a saw-whet was detected in only 1 end of a group of call points, I combined that half of the group into an owl-use site and considered the other half to be a non-use site. The area covered by the macrohabitat sites ranged from 92 ha to 460 ha, with an average size of 260 ha. I calculated the proportion of vegetation cover types at both the class and species level within each site.

In addition, I used the program FRAGSTATS (McGarigal and Marks 1995) to calculate edge density within each use and non-use site. Edge density was the sum of the lengths in meters of all edge segments within each site, divided by the total site area in hectares. I considered an edge to be any interface between forested areas (e.g., closed or open canopy forest) and non-forested areas (e.g., shrubland or herbaceous). Because edge density was based on per unit area, it facilitated comparison among sites of varying size.

Macrohabitat analysis.—I used SPSS version 14.0 for all statistical analyses. I first graphed the data and examined descriptive statistics. Given the dichotomous nature of the dependent variable (i.e., owl detection or no detection), I used stepwise logistic regression to determine which variables influenced the spatial distribution of saw-whets. I used ≤ 0.05 for probability of entry of the variable into the model and ≥ 0.10 for probability of variable removal (Pearce and Ferrier 2000, Agresti 2007). For variables deemed influential via the logistic regression analysis, I created 2x2 contingency tables and calculated the odds ratio to aid in interpreting the extent of association.

Microhabitat

Using ArcMAP, I placed 250 m radius buffers (the effective call radius from the broadcast surveys) around each small owl location to define the scale of the microhabitat. Again, due to limited detections of flammulated and northern pygmy-owl detections, I conducted this analysis only for saw-whet owls. At this scale, I considered each owl location to be a separate site and made the assumption that owl locations were activity centers (hereafter referred to as use). I repeated this procedure at randomly selected call points where I did not detect saw-whets in either year of surveys (hereafter referred to as non-use), with the assumption that these areas were not used by the owls. Using the aforementioned layers in ArcMAP, I calculated the proportion of vegetation cover types at the class and species level within each buffered area (~20 ha). With the same layers, I determined elevation, slope, and aspect. Using Hawth's Analysis Tools in ArcMAP, I calculated distance to closest roadways, streams, forest openings, and predatory owls (long-eared, great horned, and California spotted owls) relative to each

use and non-use point. To examine clustering of individuals, I looked at whether saw-whets were detected within 1000 m of other saw-whets or within 1000 m of a non-use survey point.

Because of the small owls' dependencies on snags for nesting, I measured snag characteristics (density, diameter at breast height [DBH], height, decay class, number of cavities) around each use and non-use point. I measured the characteristics in the field as this information was not available on the GIS layers. In 2006, I established 9 0.4-ha plots (100x40 m) around each owl location (15 northern saw-whet owls, 1 northern pygmy-owl, and 1 flammulated owl). Bull et al. (1990b) recommended using 0.4-ha plots in areas with <5 snags/ha, as this size was the best balance between efficiency and accuracy. Although they found standard deviation of snag densities was lower in larger plots, I decided to use 0.4 ha plots because (1) I did not know what snag densities I would encounter, (2) it would be difficult for 1 person to accurately count all snags in larger plots, and (3) I wanted to use the information in sample size analyses to determine appropriate size and number of plots for 2007. I used rectangular plots to adequately encompass the variability inherent in estimating densities of clustered individuals (Krebs 1999, Morrison et al. 2008:140), which is a typical distribution for snags (Bull 1997).

To determine snag plot locations for snag surveys in 2006, I plotted the 15 saw-whet locations in ArcMAP and centered on each a series of concentric circles of 25, 50, 100, 200, 300, 400, and 500 m radii. I calculated the proportions of class level vegetation types (i.e., closed tree canopy, open tree canopy, shrubland, herbaceous vegetation) found within each circle. The resulting line graph (Fig. 3) showed that there

was no major change in frequency of vegetation types beyond ~300 m radius. This size area was therefore a balance between surveying too small and too large an area around the owl locations while allowing for a proportionate sampling of vegetation types. I mapped all plots on ArcMAP. I centered the first plot on the point of owl detection. I arrayed 3 plots between the 100 and 200 m radii circles, with the first plot of that series randomly placed and all others equidistant. I arrayed 5 plots in a similar fashion between the 200 and 300 m radii circles (Fig. 4a). All plots ran true north.

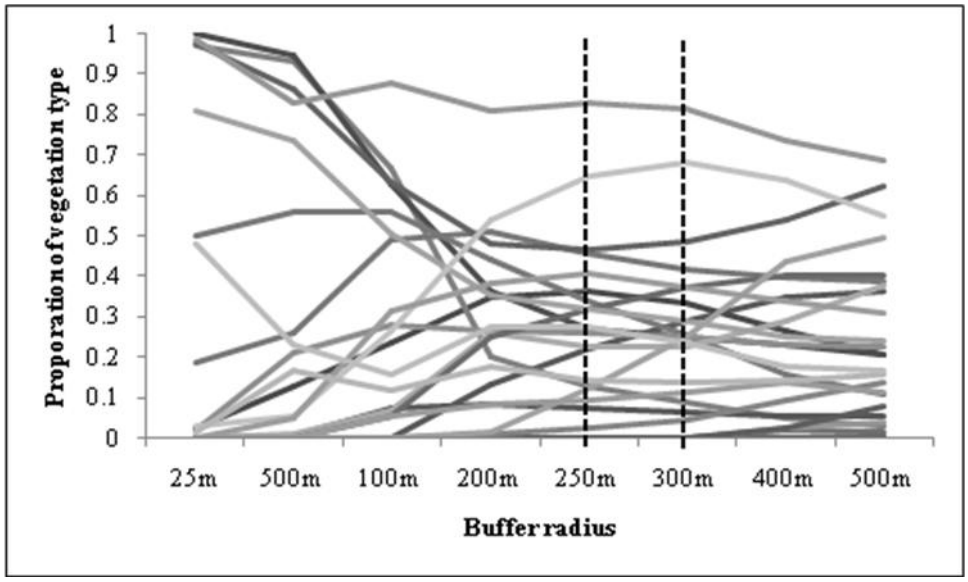

Figure 3. A depiction of the changes in the proportion of class level vegetation types at multiple spatial scales around all northern saw-whet owl detections in 2006. Changes in proportions level out (on average) between buffers of 250 m and 300 m radii (black dotted lines).

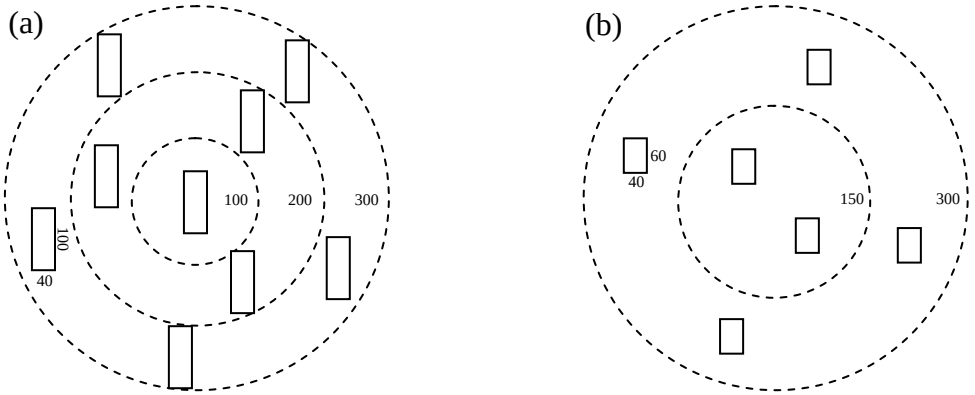

Figure 4. Diagrams of plot arrays used in (a) 2006 and (b) 2007 to sample snags in the Lake Tahoe Basin of California and Nevada. Plots were randomly distributed within the dashed circles based on a random angle from the center; therefore, each snag survey site had a unique plot array. Plot size was 40 x 100 m in 2006 and 40 x 60 m in 2007.

Within each 0.4-ha plot I counted and measured every snag, defined as standing dead trees ≥45° from horizontal, ≥13 cm DBH, and ≥1.5 m in height. Measurements to the nearest half-unit included height, DBH, and location of each snag in the plot relative to the transect line. I used the information regarding each snag's location within the plot to determine if smaller size plots would yield similar estimates of snag density, therefore saving time and effort in the 2007 field season. For each snag I also noted tree species, decay class, and number of cavities. I did not climb the snags and was therefore unable to verify the utility of all cavities counted. I visually estimated decay class on a scale of 1 to 5, with 1 indicating a newly dead snag and 5 indicating extensive decay (as per Manley and McIntyre 2004:26).

Using snag data from 2006, I conducted sample size analyses prior to the 2007 surveys (Morrison et al. 2008:122–123) as described below. Because I had measured the location of each snag in 2006, I was able to determine the number of snags per plot for all combinations of 40–100 m long and 20–40 m wide plots, in 10 m increments. For all combinations, I calculated a mean and standard error for snag density (number of snags per ha) surrounding each owl location (Fig. 5). I decided to use a plot size of 60 x 40 m in 2007 because it provided a similar mean and standard error as the 100 x 40 m plot and dramatically decreased the time and effort needed to survey each plot. I then calculated the mean and standard error of snag density at all sites based on the number of 60 x 40 m plots per site. That is, I took 10 random samples of 1 plot from all possible plots and calculated the mean and standard error. I then took 10 random samples of 2 plots from all possible plots and acquired an overall mean and standard error. I continued with the process up to 10 random samples of 10 plots. Estimates leveled out at about 6 plots per site (Fig. 6). While a greater size and number of plots would likely provide estimates of snag densities closest to reality (Bull et al. 1990b), estimates provided by 6 60 x 40 m plots appeared similar to estimates acquired with 9 100x40 m plots and allowed for a larger sample size in 2007.

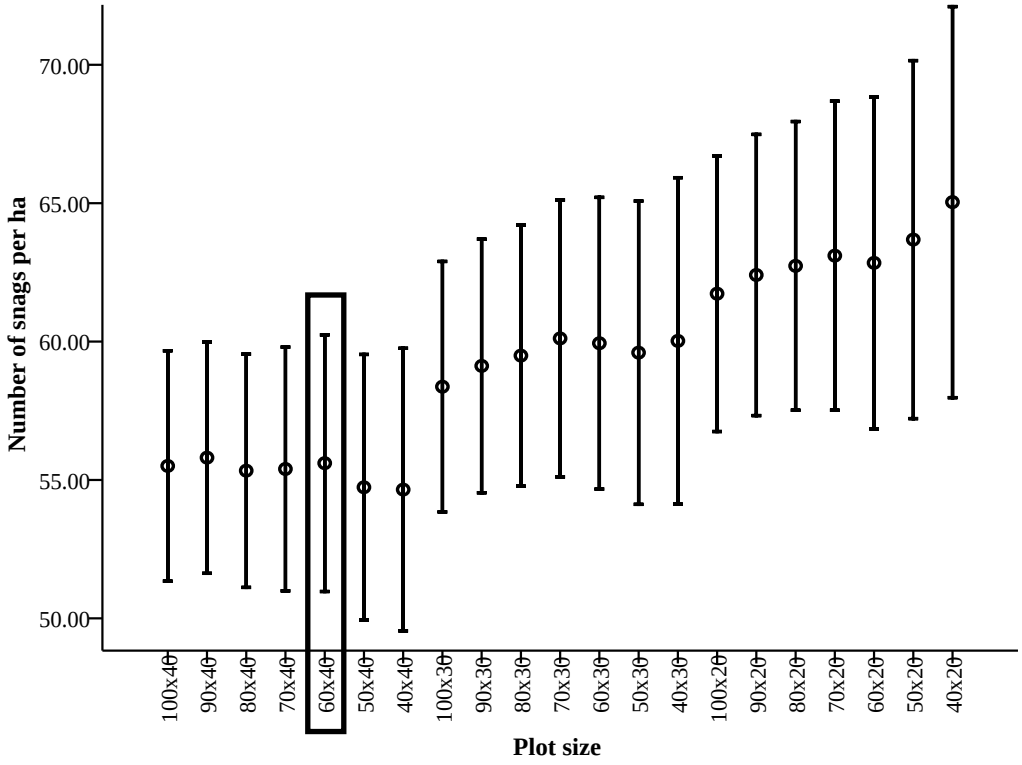

Figure 5. Comparison of the mean and standard error of snag densities (number of snags per ha) for an assortment of plot sizes. A 60 x 40 m plot size (black rectangle) provided a similar mean and standard error as the original 100 x 40 m plot size and was used for snag surveys in 2007.

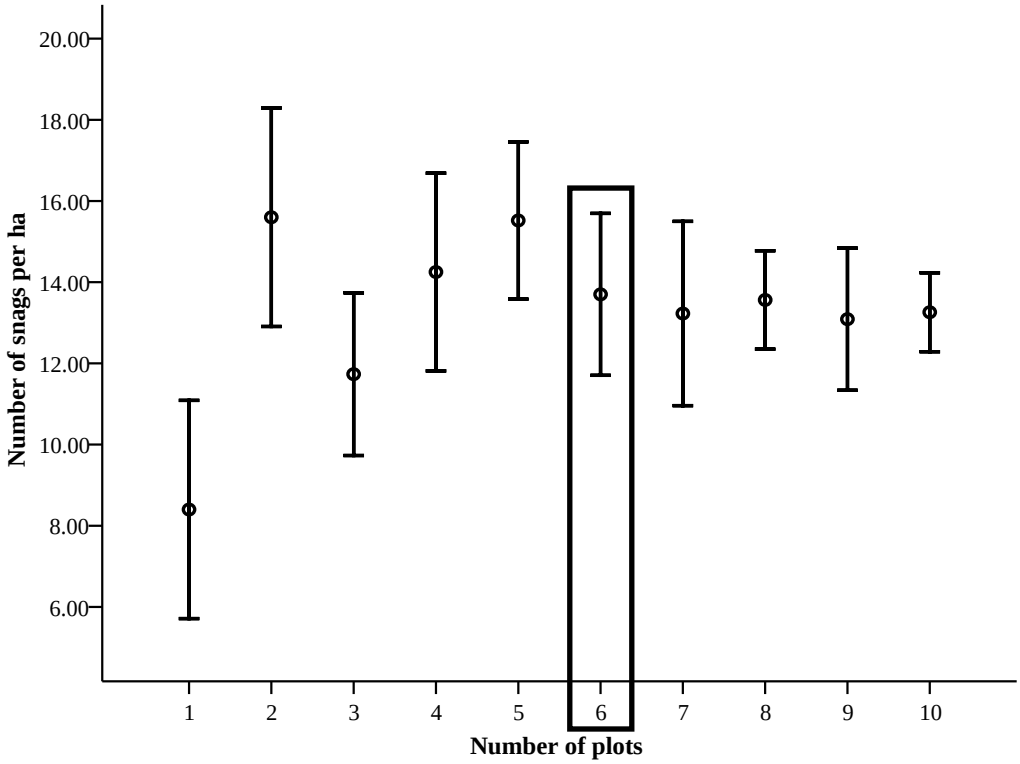

Figure 6. Mean and standard error of snag density (number of snags per ha) based on whether 1 or up to 10 60 x 40 m plots were surveyed per site. The values level out at about 6 plots per site (black rectangle), indicating that this number of plots would be sufficient for estimating snag densities in 2007.

I also conducted power analysis to determine how many sites I would need to survey to detect differences between use and non-use points (Krebs 1999). Since I found snag density to be the most variable of all snag characteristics, I used density estimates of 6 60 x 40 m plots per site in the analysis. The results of the analysis made it clear that

only large differences (e.g., >20 snag/ha) in snag densities would be discernible with the number of plots realistically surveyed in the 2 years (Table 1).

Table 1. Results of power analysis indicating necessary sample sizes for detecting differences in snag densities given a range of values for effect size, alpha, and power. Sample sizes are for a 2-sided test. Data are from snag surveys in 2006.

	Effect size	**Alpha**	**Power**	**Sample size**
Mean = 73.07	5	0.1	0.8	580
SD = 34.22	5	0.15	0.8	488
	5	0.2	0.8	423
	10	0.1	0.8	145
	10	0.15	0.8	122
	10	0.2	0.8	106
	15	0.1	0.8	65
	15	0.1	0.9	90
	15	0.15	0.8	55
	15	0.15	0.9	78
	15	0.2	0.8	47
	15	0.2	0.9	69
	20	0.1	0.8	37
	20	0.1	0.9	51
	20	0.15	0.8	31
	20	0.15	0.9	44
	20	0.2	0.8	27
	20	0.2	0.9	39

Thus, in 2007 I used 6 60 x 40 m plots arrayed around each owl location. I arrayed 2 plots between the 150 m radius circle, with the first plot of that series placed based on a random angle value, and the second plot at +180°. I arrayed 4 plots in a similar fashion between the 150 and 300 m radii circles (Fig. 4b). All plots ran true north. I measured the same variables as in 2006 except for snag location in the plot.

Within the same plots as the snag surveys, I also assessed ground cover. Ground cover was another habitat feature not captured in the GIS layers and could prove informative when analyzing owl occurrences, as it affects the owl's ability to detect and capture ground-dwelling prey (e.g., small mammals). I used the point intercept method along the centerline of each plot and recorded ground cover at every other meter, starting at 1 m. From this method, I calculated the percent cover for each of 15 categories (Table 2). Because most categories comprised a small percentage of all data points, I decided to combine several categories into more general "open" versus "covered" ground based on how the ground would be perceived by an owl (Table 2). That is, the ability of an owl to detect prey (e.g., small mammal) would presumably be limited in an area of ground covered by shrubs, logs, and herbaceous vegetation (i.e., "covered" ground) while prey would be more accessible in areas covered primarily by leaf litter or bare ground (i.e., "open" ground).

I surveyed snags and ground cover at different locations in 2006 and 2007 and combined the data from both years, resulting in 40 use and 40 non-use sites. Snag and ground cover surveys in 2006 were at areas of small owl use; surveys in 2007 were at both use and non-use areas.

Table 2. Ground cover categories grouped into open versus covered ground.

Open ground	Covered ground
Trail	Log
Bare ground	Herbaceous
Dirt road	Tree sapling
Leaf litter	Shrub
Stump	Tree (low branches)
Rock	
Paved road	
Woody debris	

Microhabitat analysis.—I used SPSS version 14.0 for all statistical analyses. I first graphed the data and examined descriptive statistics. I examined the following variables: proportions of class- and species-level cover types, snag characteristics, ground cover, occurrence of conspecific neighbors, distance from use or non-use points to roadways, waterways, forest clearings (i.e., edge), and predatory owls, along with elevation, slope, and aspect. I categorized the values for each variable prior to running logistic regression. I split elevation into 3 categories based on Manley et al.'s (2000) description of major vegetation zones. I segregated distance to owl predators into 2 categories: <2000 m and >2000 m. I split mean percent cover of vegetation classes into 5 categories of 20% increments. Based on natural breaks in the data, I split mean percent cover of dominant tree species into 3 categories: 0–5%, 6–50%, and >50%. I then used stepwise logistic regression to determine which variables influenced the spatial distribution of saw-whets at the microhabitat scale. For variables deemed influential via the logistic regression analysis, I created 2 x 2 contingency tables and calculated the odds ratio to aid in interpreting the degree of association.

In addition, I conducted t-tests and ANOVA tests to determine how snag densities and ground cover may vary throughout the basin depending on the surrounding dominant tree species, regardless of owl occurrence.

Nest searching

Also at the microhabitat scale, I intended to quantify breeding success or failure of the small, cavity-nesting owls. In 2006, I attempted to relocate any small owl that was detected during the nocturnal surveys. In the early morning or late afternoon following the detection, I returned to the area in which the owl was originally detected. I typically surveyed an area $\geq$500 m^2 in a systematic fashion. I attempted to initiate a response from the owl by broadcasting the appropriate owl calls. I knocked and scratched on trees that contained cavities to try and flush any species that might be nesting within (Goggans 1986, Bonar 2000) and searched for signs of owl presence and activity. My intentions were to find and monitor each owl to determine whether it was paired and whether it was breeding. However, I seldom rediscovered owls during the follow-up surveys and located no nests. In 2007, I decreased considerably the amount of time spent on follow-up surveys and only searched for nests in areas where I detected pairs of owls (and thus had a higher probability of containing a nest). Although once again I was unable to locate nests, I did detect 3 juvenile northern saw-whet owls in survey areas throughout the summer (see Results).

RESULTS

Broadcast surveys

I surveyed 225 points in 2006 and 2007. Across both years I detected 5 flammulated owls, 5 northern pygmy-owls, 52 northern saw-whet owls (Fig. 7, Table 3). I also detected 1 long-eared owl, 27 great horned owls, and 7 California spotted owls (Table 3). Saw-whets were the only species detected in sufficient numbers for statistical analysis, although I have provided some qualitative descriptions of flammulated owl and northern pygmy-owl locations.

Detection probability

Although the probability of detecting a saw-whet remained relatively low throughout the study, probabilities were higher in 2007 than in 2006 due in part to the higher total number of individuals detected (i.e., 37 saw-whets in 2007 versus 15 in 2006) (Table 4). Of the call points surveyed in both years, detection probability was 2 and 6 times higher in 2007 with 6 and 3 visits, respectively. Detection probability in 2007 among all call points did not increase with an increase in the number of visits. At best, with each visit to a call point, I had a probability of 0.25 of detecting a saw-whet if it occurred in the vicinity of the call point. Among all call points surveyed, the overall probability of occupancy was low (i.e., 52 occupied sites / 225 total sites = 0.23). That is, the probability of a saw-whet occupying the area near any given call point was 0.23.

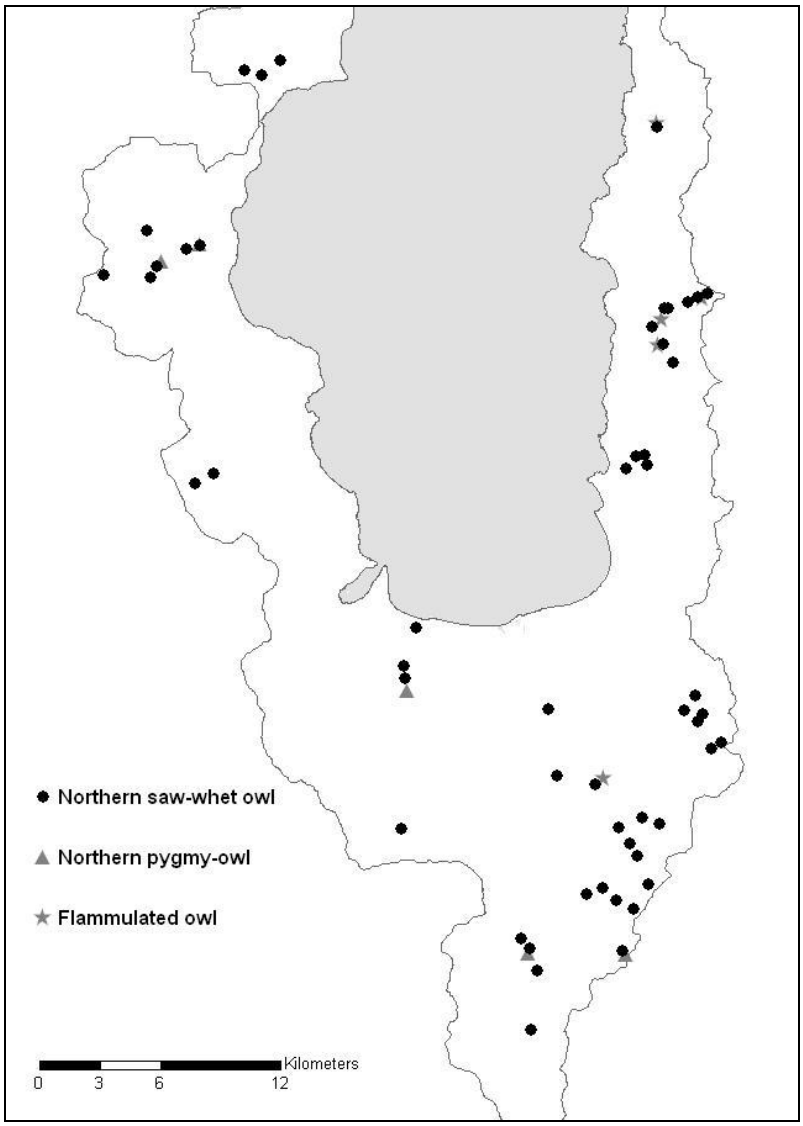

Figure 7. Locations of small, cavity-nesting owls detected during nocturnal broadcast surveys and incidentally in Lake Tahoe Basin, California and Nevada, May–July 2006 and March–June 2007.

Table 3. Number of individual owls detected in Lake Tahoe Basin, California and Nevada, May–July 2006 and March–June 2007 during nocturnal broadcast surveys and incidentally.

	Flammulated		Northern pygmy		Northern saw-whet		Long-eared		Great horned		California spotted	
	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007
Survey detections	1	4	0	3	14	38	0	1	11	13	3	2
Incidental detections	0	0	1	1	1	2	1	0	2	2	1	1

Table 4. Detection probabilities for northern saw-whet owls for all call points and for the subset of call points that were surveyed both years.

	All call points				Call points surveyed both years			
	May–July 2006		March–June 2007		May–July 2006		March–June 2007	
# of surveys	3	6	3	6	3	6	3	6
# of call points	132	77	137	44	56	34	56	34
Detection probability	0.035	0.073	0.253	0.245	0.036	0.117	0.131	0.226

Macrohabitat

I examined 25 use sites and 9 non-use sites at the macrohabitat scale. Plots of confidence intervals for cover class showed extensive overlap in mean values between areas of use and non-use (Fig. 8) and less overlap in the average percent cover of Jeffreypine, red fir, and white fir (Fig. 9). All other shrub and tree species averaged less than 6% cover and were not included in the analysis. 'Percent of area' in these figures refers to the amount of area within the site categorized as a particular cover type. Thus,

on average, ~10% of the area within the use sites contained the closed canopy cover type while 70% of the area contained open canopy cover type (Fig. 8). Although edge density was 16% higher for non-use than used sites (Table 5), there was high variability among all sites (Fig. 10). Larger values for edge density indicated a greater extent of edge in the area of interest. Based on the aforementioned plots, I decided to include only the percent cover of Jeffrey pine, red fir, and white fir in logistic regression. Logistic regression selected the percent cover of white fir as negatively influencing the presence of northern saw-whet owls ($P = 0.021$), with overall percentage of correct predictions of 76.5%. The odds ratio for the occurrence of saw-whets in areas not dominated by white fir was 6.33. This was determined by categorizing the percent of area dominated by white fir into <30% or >30% for the 2 x 2 contingency tables. Thus, I was ~6 times more likely to detect a saw-whet at sites with <30% of the area dominated by white fir than at sites with >30% of the area dominated by white fir.

Microhabitat

I examined 52 use and 40 non-use sites at the microhabitat scale. Sample sizes differed slightly, however, depending on the methods employed to measure the variables (Table 6). As with the macrohabitat scale, there was extensive variability and overlap of the data acquired at locations with and without owl detections (Table 6). On average, I detected saw-whets at locations 100 m higher in elevation than non-use points (Fig. 11). I detected 31% of saw-whets on west-facing slopes, with another 28% on north-facing slopes; 20% more owl use points were located on west-facing slopes than non-use points (Fig. 12). The degree of slope for use and non-use points were similar, with the primary

difference being that ~10% more owl use points were located on relatively steep slopes (>60°) than non-use points (Fig. 13). Nearly half of the saw-whets, however, were located on 11–30° slopes.

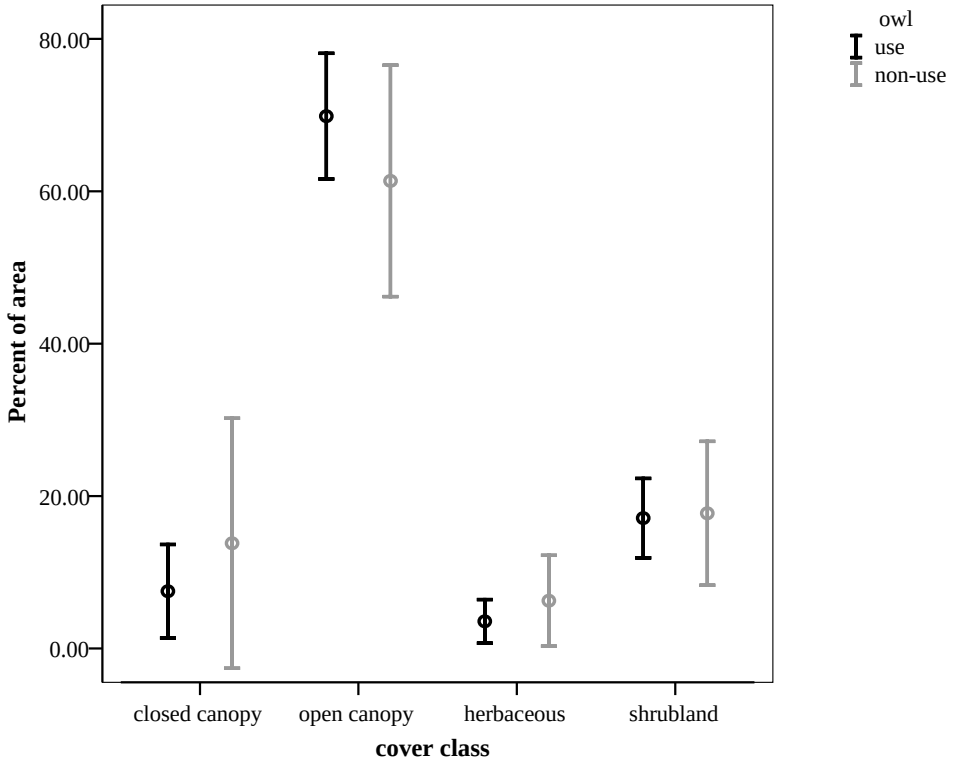

Figure 8. Mean percent area and corresponding 95% confidence intervals encompassed by particular cover classes at macrohabitat sites of use and non-use.

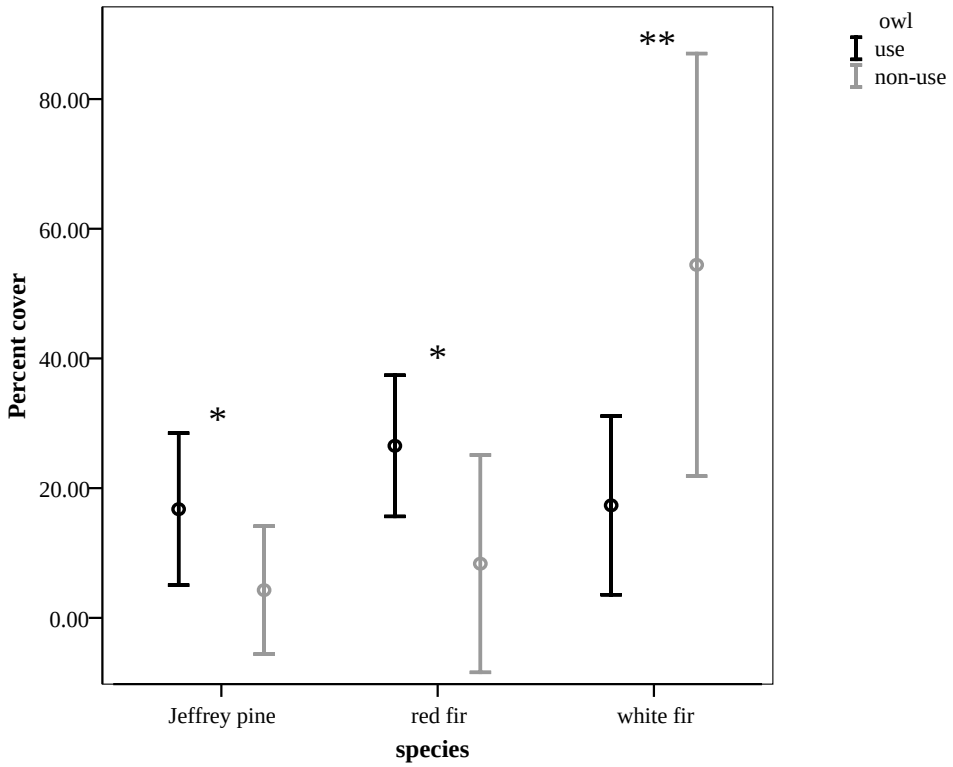

Figure 9. Mean percent cover and corresponding 95% confidence intervals of tree species at macrohabitat sites of use and non-use. A single asterisk indicates $0.05 \leq P \leq 0.10$; double asterisks indicate $P \leq 0.05$.

Table 5. Sample sizes, statistics, and *P* values for mean comparison of macrohabitat variables in areas of owl use and non-use.

	Owl Use					Owl Non-use					
	N	**Mean ± SD**	**Min**	**Max**	**Median**	***N***	**Mean ± SD**	**Min**	**Max**	**Median**	***P* value**
Edge density	25	58.1 ± 39.0	5.6	136.0	54.0	9	67.4 ± 37.9	16.2	130.3	55.0	0.540
% Class cover:											
Closed canopy	25	7.5 ± 14.9	0.0	69.1	2.5	9	13.8 ± 21.3	0.7	54.8	1.9	0.340
Open canopy	25	69.9 ± 20.0	25.6	97.1	77.9	9	61.4 ± 19.7	37.6	96.6	58.5	0.281
Herbaceous	25	3.6 ± 6.9	0.0	26.9	1.0	9	6.2 ± 7.8	0.0	22.6	2.4	0.338
Shrubland	25	17.1 ± 12.6	1.5	54.8	14.2	9	17.7 ± 12.3	1.9	38.4	17.1	0.897
% Cover by tree spp:											
Jeffrey pine	25	16.8 ± 28.4	0.0	84.2	0.0	9	4.3 ± 12.8	0.0	38.5	0.0	0.089
Red fir	25	26.5 ± 26.4	0.0	81.0	29.5	9	8.4 ± 21.8	0.0	65.9	0.0	0.074
White fir	25	17.3 ± 33.4	0.0	97.1	0.0	9	54.4 ± 42.4	0.0	98.1	71.4	0.012

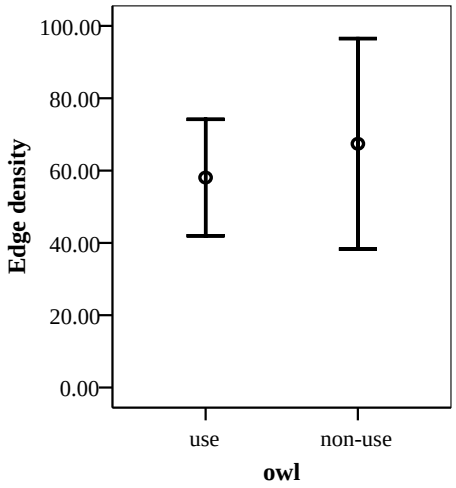

Figure 10. Mean edge density (i.e., total length [m] of edge divided by total area [ha]) and corresponding 95% confidence intervals at macrohabitat sites of use and non-use.

Table 6. Sample sizes, statistics, and *P* values for mean comparison of microhabitat variables in areas of owl use and non-use.

	Owl Use					Owl Non-use					
	N	**Mean ± SD**	**Min**	**Max**	**Median**	***N***	**Mean ± SD**	**Min**	**Max**	**Median**	***P* value**
Elevation (m)	52	2292 ± 253	1902	2813	2307	40	2192 ± 262	1902	2844	2143	0.065
Distance to (m):											
Forest opening	52	93 ± 111	0	508	61	40	91 ± 144	0	700	14	0.931
Stream	52	438 ± 451	2	2095	263	40	542 ± 558	18	1907	265	0.330
Paved road	52	2490 ± 1728	184	6061	1917	40	2149 ± 1790	4	5902	1838	0.359
Owl predators	52	2598 ± 2561	29	9944	1464	40	1965 ± 2145	171	10520	1341	0.201
% Class cover:											
Closed canopy	49	11.3 ± 21.9	0.0	99.5	0.0	38	9.7 ± 21.9	0.0	94.6	0.0	0.727
Open canopy	49	69.6 ± 27.7	0.0	100	82.3	38	61.7 ± 29.2	0.0	100	68.6	0.192
Herbaceous	49	3.2 ± 7.5	0.0	37.7	0.0	38	5.8 ± 12.0	0.0	62.6	0.0	0.244
Shrubland	49	15.6 ± 15.0	0.0	64.6	11.7	38	22.1 ± 24.5	0.0	87.7	14.3	0.144
% Cover by tree spp:											
Jeffrey pine	49	16.5 ± 32.8	0.0	97	0.0	38	10.6 ± 25.1	0.0	100	0.0	0.342
Lodgepole pine	49	7.6 ± 17.3	0.0	82	0.0	38	4.1 ± 13.8	0.0	80.5	0.0	0.309
Red fir	49	24.4 ± 30.5	0.0	93.9	0.6	38	7.6 ± 18.5	0.0	71.5	0.0	0.002
Subalpine conifer	49	7.1 ± 12.1	0.0	42	0.0	38	5.2 ± 14.2	0.0	57.1	0.0	0.511
White fir	49	16.5 ± 33.2	0.0	100	0.0	38	40.2 ± 42.1	0.0	100.0	22.0	0.006
Snag characteristics:											
# snags/ha	40	41.1 ± 25.2	5.6	106.9	37.5	40	46.0 ± 35.9	0.7	168.1	36.1	0.479
# snags/ha ≥ 30 cm DBH	40	24.5 ± 14.7	2.8	73.6	21.5	40	25.0 ± 17.0	0.7	70.1	22.6	0.880
# snags/ha ≥ 40 cm DBH	40	16.2 ± 10.1	2.1	46.5	14.6	40	16.6 ± 11.8	0	43.8	15.6	0.861
# snags/ha with cavities	40	3.1 ± 3.4	0.0	18.1	1.7	40	2.5 ± 3.0	0.0	15.3	1.4	0.414
Total # cavities/ha	40	5.0 ± 5.9	0.0	29.9	2.8	40	3.6 ± 4.2	0.0	22.2	2.4	0.220
# snags/ha > decay class 1	40	24.4 ± 19.3	1.4	80.6	20.5	40	23.5 ± 22.6	0.0	104.2	18.4	0.854
Snag DBH (cm)	40	42.2 ± 12.2	24.6	90.9	39.4	40	38.9 ± 8.5	25.1	55.5	38.4	0.165
Snag height (m)	40	10.5 ± 2.3	7.1	16.6	10.5	40	9.6 ± 2.2	5.7	18.0	9.3	0.074
% Open ground	40	61.0 ± 17.7	22.7	97.3	60.6	40	53.4 ± 19.7	13.4	90.6	53.9	0.074

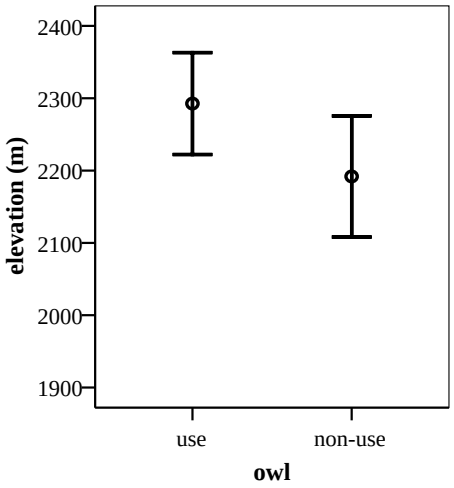

Figure 11. Mean elevation and corresponding 95% confidence interval among points of use and non-use.

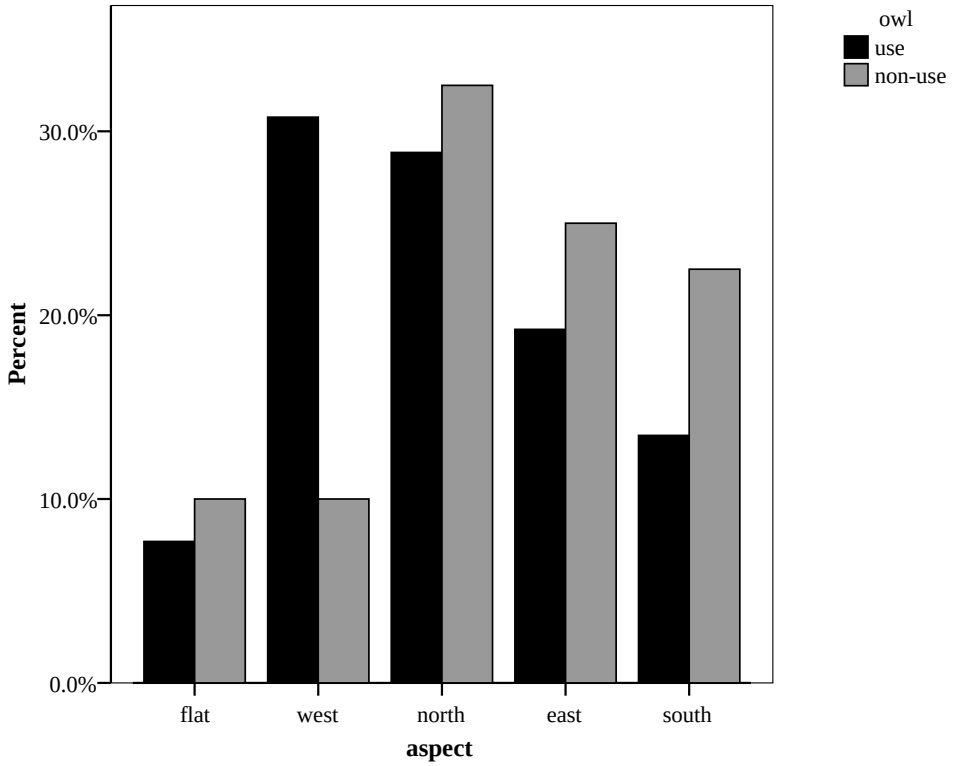

Figure 12. Percent of use and non-use points located at the specified aspect.

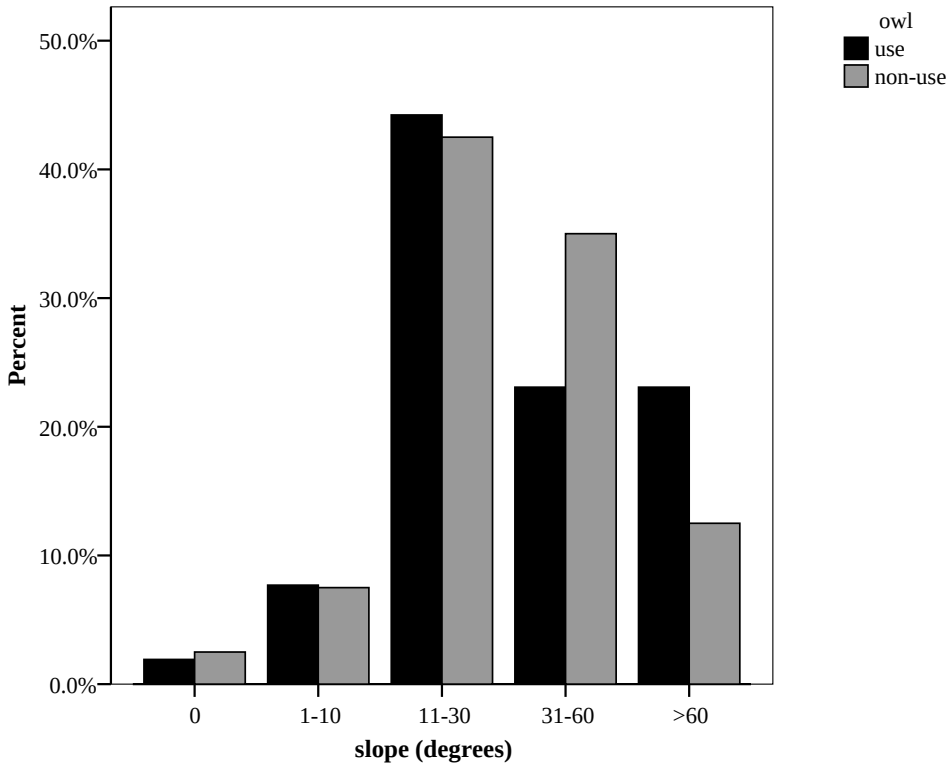

Figure 13. Percent of use and non-use points located at the specified slope.

Distances to certain physical features or other owls showed extensive variability and overlap between areas of use and non-use. Although not statistically significant, on average I detected saw-whets ~630 m further from predatory owls and ~340 m further from paved roads than non-use points (Fig. 14).

The number of snags per ha included all snags ≥ 13 cm DBH and ≥ 1.5 m high and were similar between use and non-use points (Fig. 15). There was also no difference in snag densities when comparing the number of large snags (Table 6). The number of snags with cavities, average snag size, and snag species were likewise similar between use and non-use points (Figs. 15–17). Although the percent of open ground was ~12% lower in non-use areas, there was nevertheless a wide range of variability and the values were not statistically different (Fig. 18 and Table 6).

The percent of area dominated by particular cover classes showed similar extents between sites of use and non-use (Fig. 19). Categorizing the cover class data, however, into 20% increments indicated potential differences in locations with a high proportion (>80%) open canopy cover and low proportion (<20%) of shrubland cover (Fig. 20 and 21, respectively). Of the dominant tree species (Fig. 22), the percent of area covered by red fir and white fir showed significant differences between areas of use and non-use ($P = 0.002$ and $P = 0.006$, respectively) (Table 6). I detected saw-whets at 13% of the call points in areas dominated by white fir, versus 29% of the call points in areas where white fir did not dominate. Conversely, I detected saw-whets at 32% of the call points in areas dominated by red fir, versus 17% of the call points where red fir did not dominate.

I used the aforementioned categories of open canopy cover, shrubland cover, red fir and white fir percent cover in the logistic regression analysis.

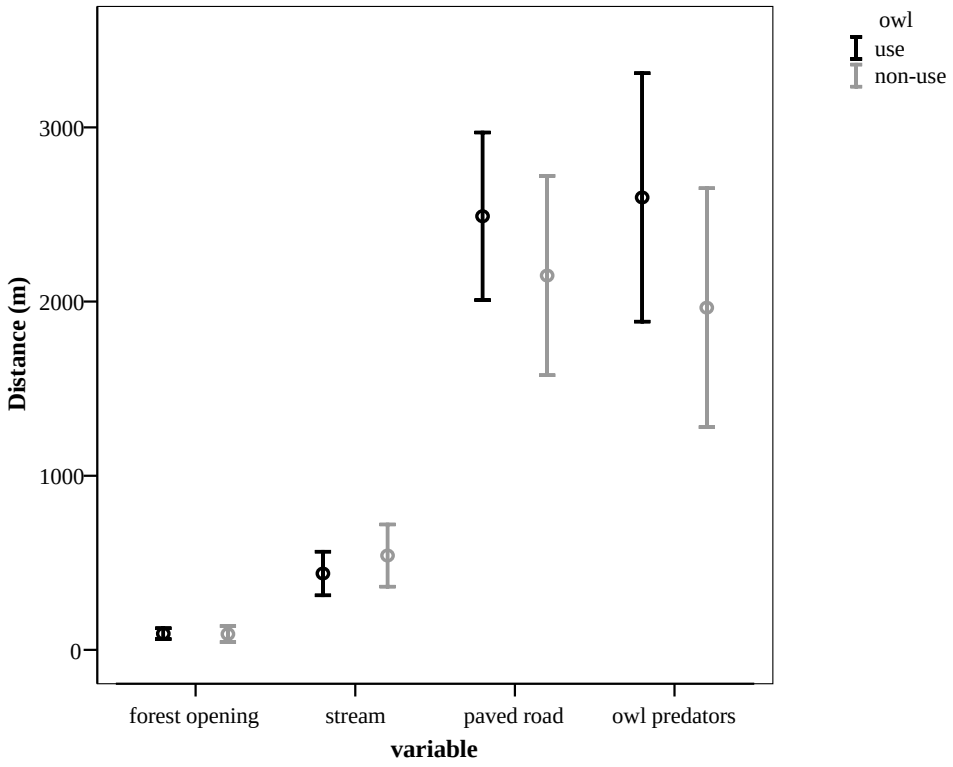

Figure 14. Mean distances and corresponding 95% confidence intervals between use or non-use points and forest openings, streams, paved roads, or owl predators.

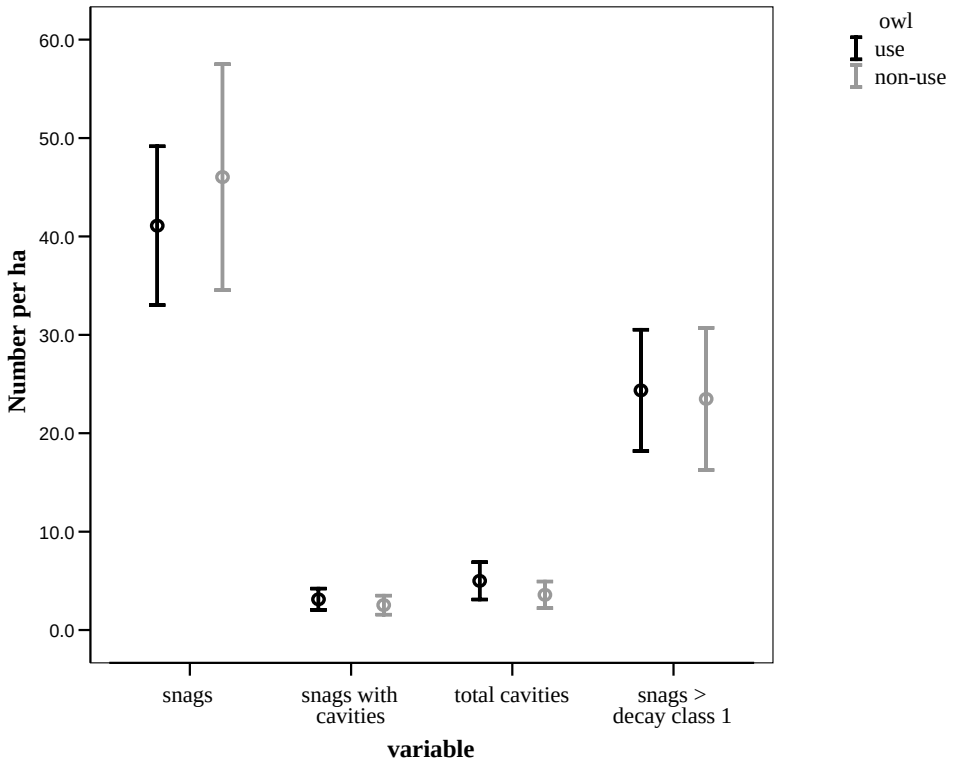

Figure 15. Mean densities and corresponding 95% confidence intervals of snags with specified characteristics at use and non-use sites.

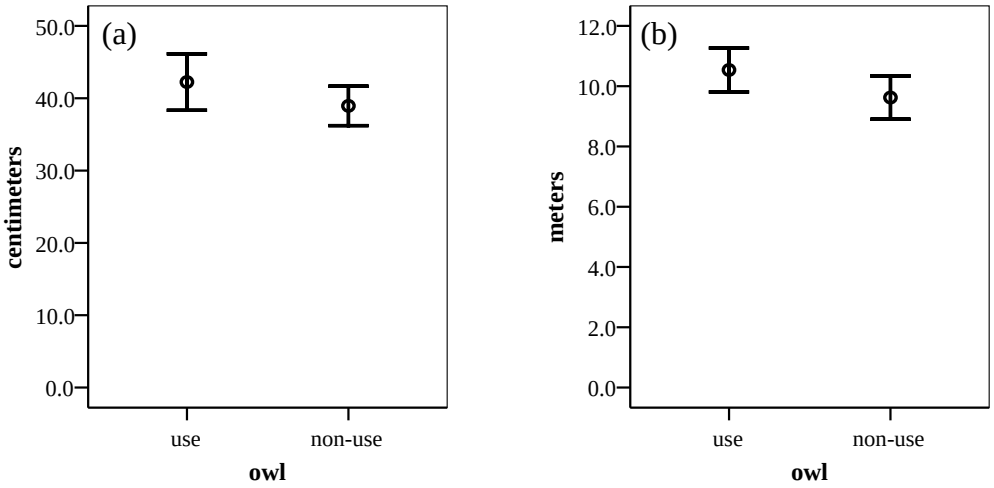

Figure 16. Mean diameter at breast height (a), mean height (b), and corresponding 95% confidence intervals of snags at use and non-use sites.

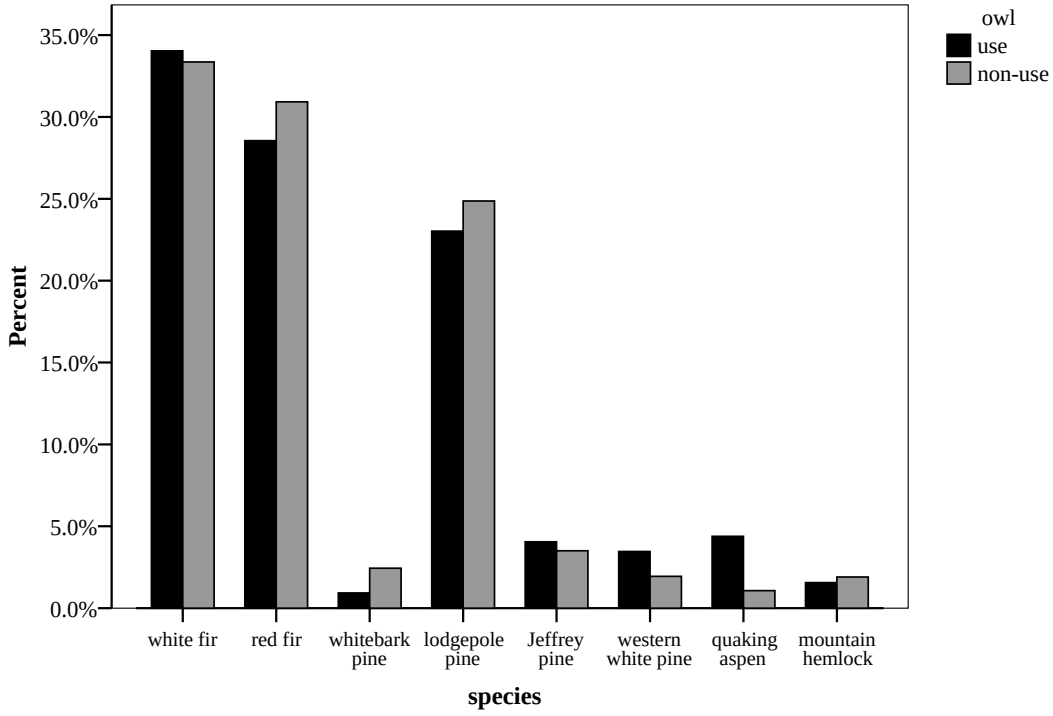

Figure 17. Percent of snags of each tree species at use and non-use sites.

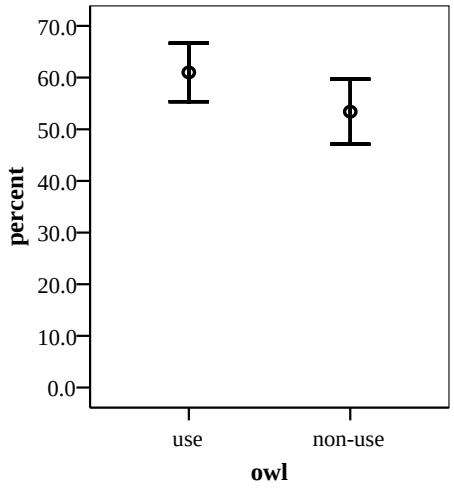

Figure 18. Mean percent and corresponding 95% confidence intervals of open ground at use and non-use sites.

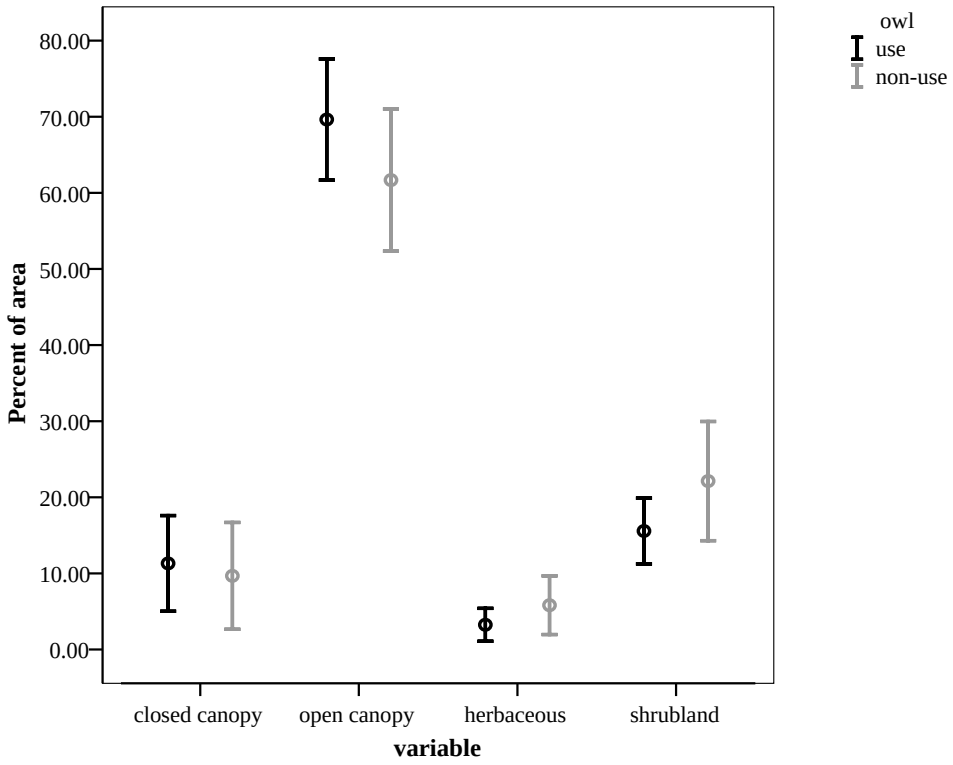

Figure 19. Mean percent area and corresponding 95% confidence intervals encompassed by particular cover classes at microhabitat sites of use and non-use.

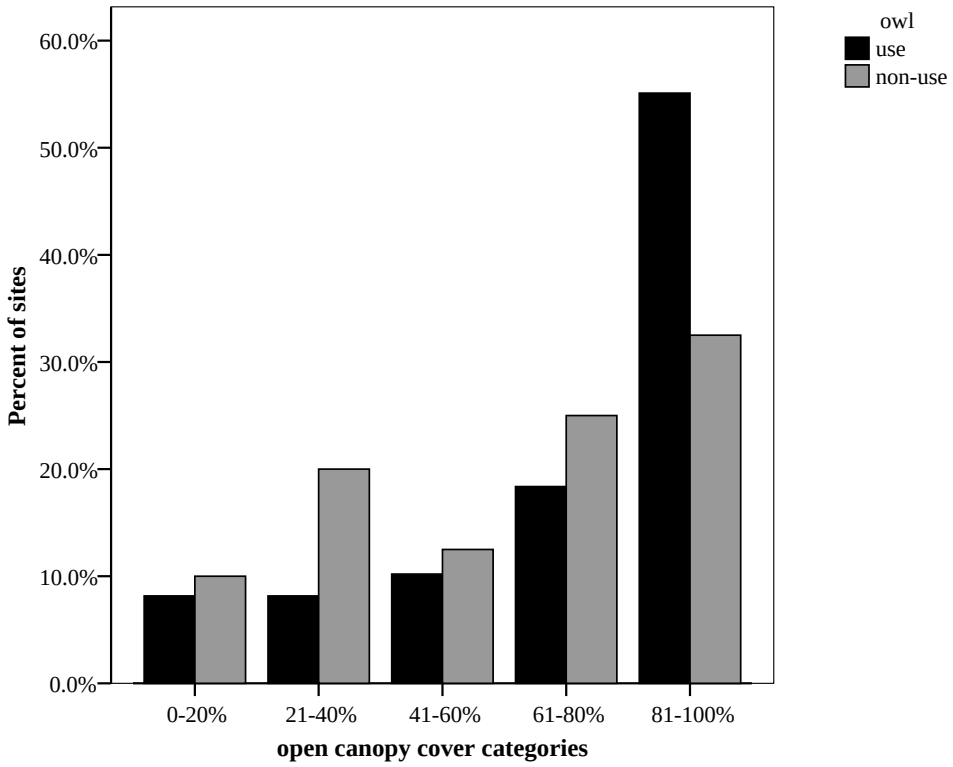

Figure 20. Percent of microhabitat sites containing the given category of open canopy cover.

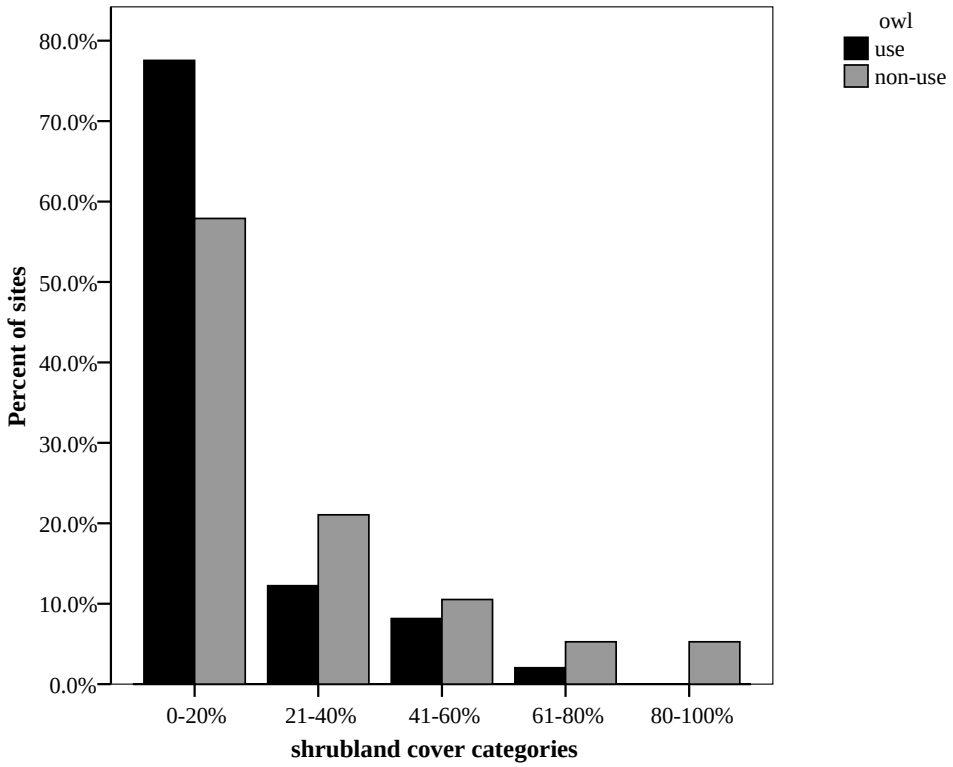

Figure 21. Percent of microhabitat sites containing the given category of shrubland cover.

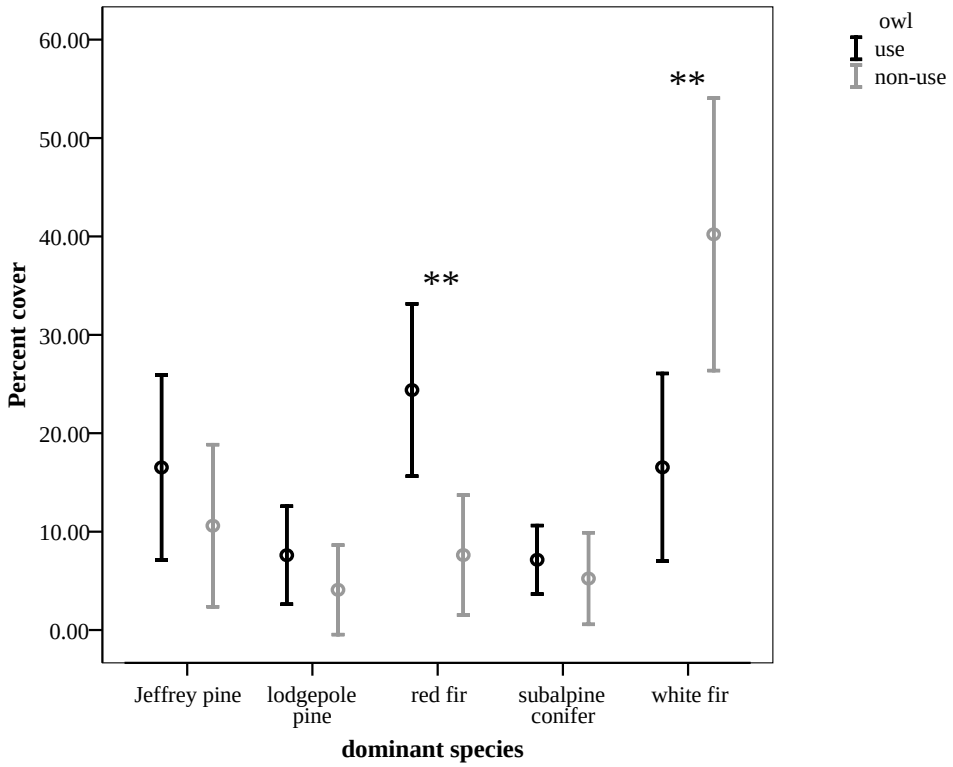

Figure 22. Mean percent cover and corresponding 95% confidence intervals of dominant tree species at use and non-use sites. All other shrub and tree species comprised <5% of the area within each site. Double asterisks indicate $P \leq 0.05$.

As with macrohabitat, logistic regression revealed the percent cover of white fir was negatively correlated with the presence of saw-whets ($P = 0.007$) whereas the percent of shrubland was negatively correlated with saw-whet presence (($P = 0.006$). Overall percentage of correct predictions was 69.0%. The odds ratio for the occurrence of saw-whets in areas not dominated by white fir was 3.90. Thus, I was ~4 times more likely to detect a saw-whet in areas without white fir than in areas with white fir. The odds ratio for the occurrence of saw-whets in areas containing less than 20% shrubland cover was 2.51. Thus, I was ~2.5 times more likely to detect saw-whets in areas not dominated by shrubland.

Regardless of owl occurrence, mean snag density and open ground cover differed in areas of the basin containing different dominant tree species. Results indicated a statistically significant difference ($P = 0.001$) in snag density, with an average of 24 more snags per ha found in areas dominated by white fir (primarily the west side of the basin) than in areas dominated by either red fir or Jeffrey pine (Fig. 23). The percent of open ground cover likewise differed significantly ($P = 0.001$) among sites dominated by Jeffrey pine, white fir, or red fir (Fig. 24). On average, open ground comprised ~45%, ~55%, or ~65% of the area dominated by Jeffrey pine, white fir, or red fir, respectively.

I analyzed owl clustering with logistic regression separate from the other habitat variables. The analysis indicated the occurrence of 1 saw-whet was influenced by the occurrence of a neighboring saw-whet ($P = 0.021$). The 2 x 2 contingency table consisted of owl or no owl versus neighbor or no neighbor. The odds ratio showed I was

2.74 times more likely to find a saw-whet within 1000 m of another saw-whet than within 1000 m of a non-use point.

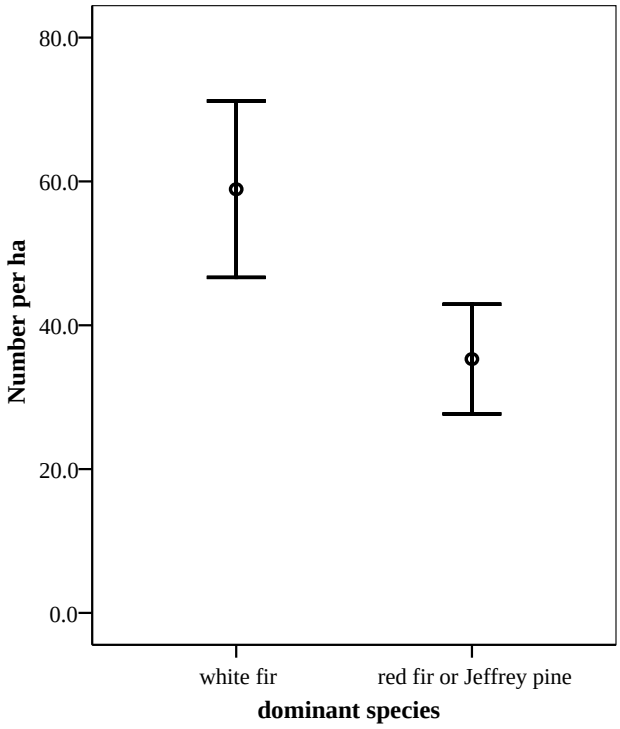

Figure 23. Mean number of snags per ha and corresponding 95% confidence intervals for sites dominated by white fir versus sites dominated by red fir or Jeffrey pine.

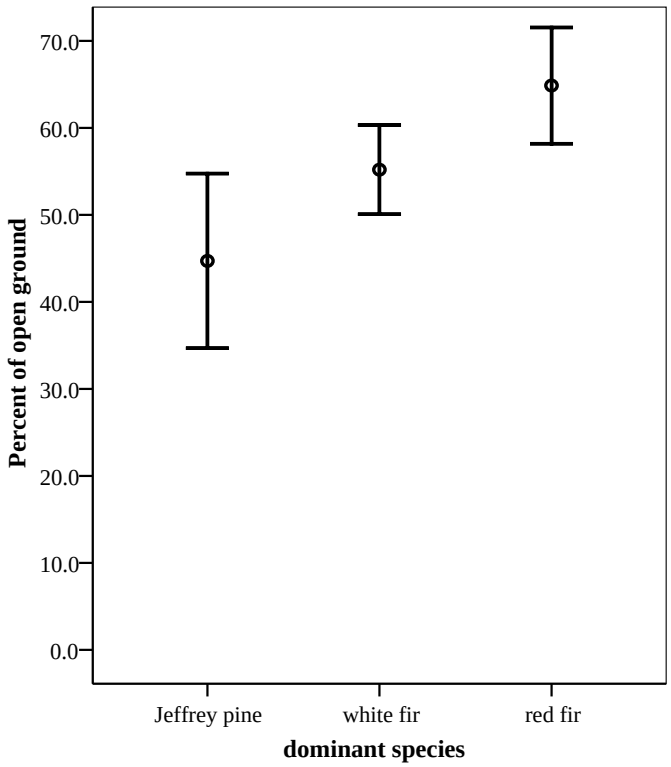

Figure 24. Mean percent of open ground and corresponding 95% confidence intervals for sites dominated by Jeffrey pine, white fir, or red fir.

Flammulated owl

I detected 5 flammulated owls during the 2 seasons of surveys (Fig. 7). One individual was found in the southern section of the basin at a low elevation site at the end of June 2006. The other 4 individuals were located on the east side of the basin at mid-elevations and detected from mid- to late May 2007. Locations in which the flammulated owls occurred were comprised of a relatively high proportion of quaking aspen snags (Fig. 25) – 30% versus less than 5% at non-use areas – although this

observation was based on a small sample size. Snags per ha averaged 42.36 across the 5 sites, with 1.94 snags/ha containing at least 1 cavity.

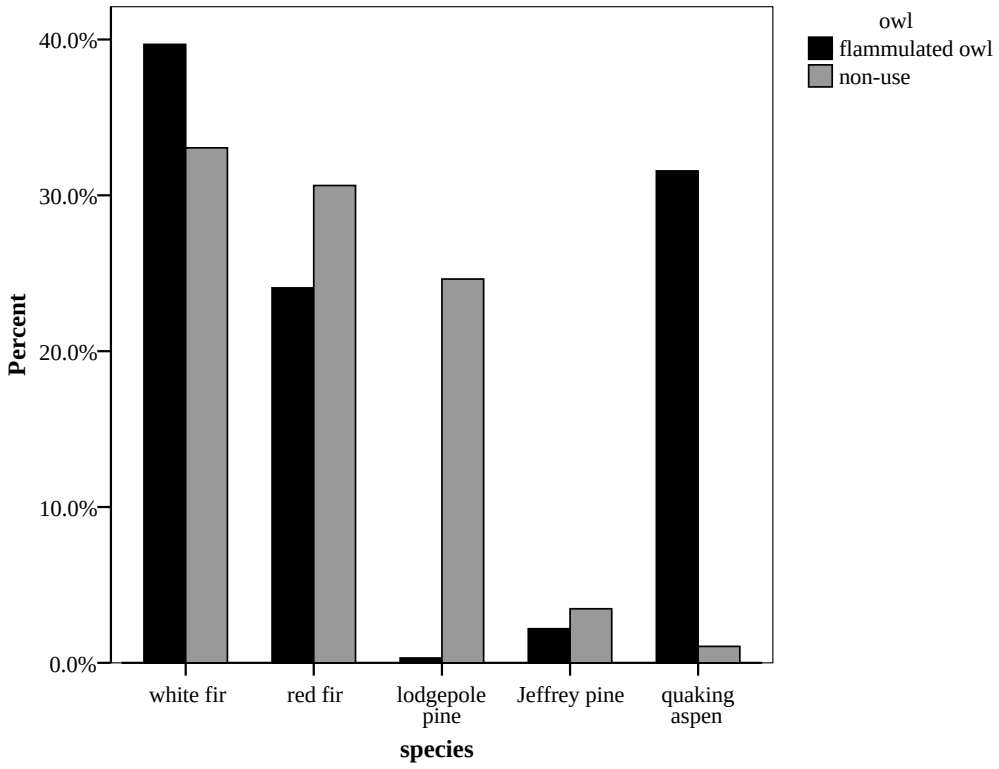

Figure 25. Percent of snags of each tree species at flammulated owl use and non-use sites (non-use data is the same as used for the northern saw-whet analysis).

Northern pygmy-owl

I detected 5 northern pygmy-owls during the 2 years of surveys in the western and southern sections of the basin (Fig. 7), 2 of which were incidental observations (i.e., not detected during the nocturnal surveys). One individual was detected at a mid-elevation

site with the other 4 individuals located in low elevation sites. I detected the owls periodically between March and June both years. Areas occupied by northern pygmy-owls were comprised of ~25% more white fir snags and ~20% fewer red fir snags than areas without pygmy-owl detections (Fig. 26). Snags per ha averaged 36.11 across the 5 sites, with 4.58 snags/ha containing at least 1 cavity.

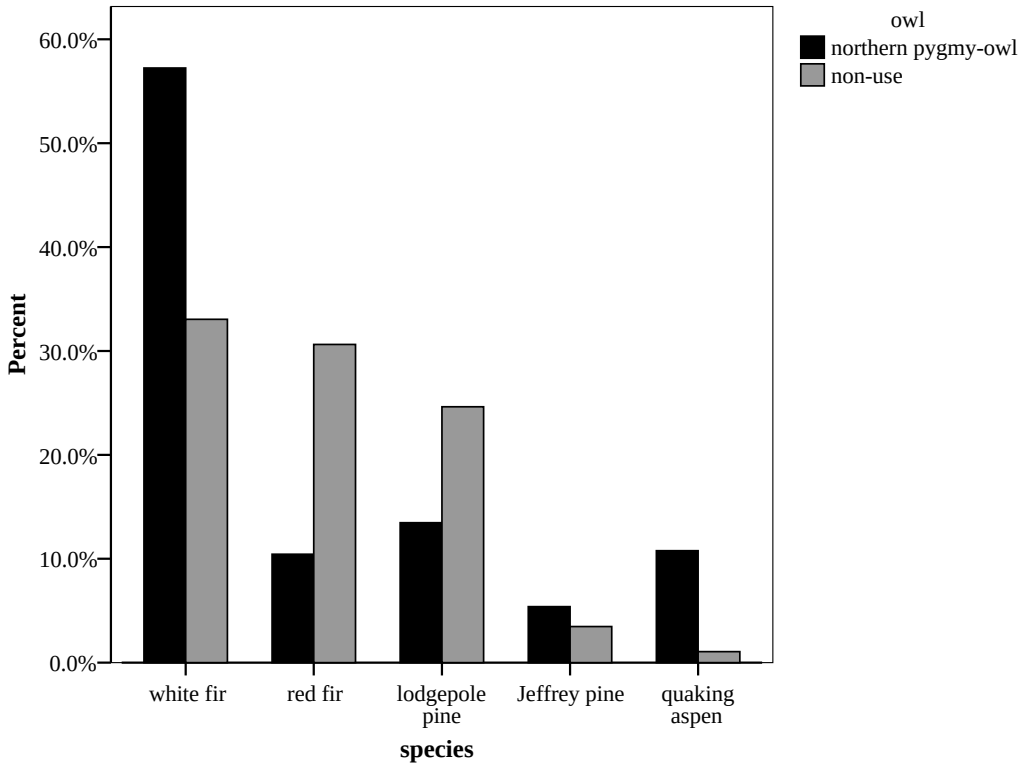

Figure 26. Percent of snags of each tree species at northern pygmy-owl use and non-use sites (non-use data is the same as used for the northern saw-whet analysis).

Nest searching

Although I was unable to find nests in the 2 seasons of surveys, I did discover 3 juvenile saw-whets incidentally at 3 different areas in 2007. I found one at a low elevation east-side site on 27 June, and the other 2 at mid-elevation southern sites on 11 and 17 July. All 3 juvenile locations were close to or within saw-whet microhabitat sites.

DISCUSSION

Broadcast surveys

Nocturnal broadcast surveys indicated that northern saw-whet owls are common in LTB relative to other owl species, although their distribution is patchy. Saw-whets are noted as uncommon to common throughout their range in California (CWHR 2000). The number of saw-whets detected during my study was greater than expected by the U.S. Forest Service (V. Lyon, personal communication). Lack of adequate owl surveys prior to my study limits the discussion of trends in relative abundance or distribution. However, in the Eldorado National Forest (adjacent to and southwest of the LTB), saw-whets were the most common incidental species detected during California spotted owl surveys (Crozier et al. 2003). They were also "relatively numerous and widespread" in the Glass Mountain region of east-central Sierras (southeast of the LTB) (Shuford and Fitton 1998:17).

Flammulated owls and northern pygmy-owls were scarce during my 2 seasons of surveys. Owl surveys conducted in the LTB and Eldorado National Forest in 2001 found higher numbers of flammulated and northern pygmy-owls at elevations of 915–1,525 m, although the total number of individuals was relatively low (9–11 individuals) (Manley et al. 2002); these elevations are lower than what is available in the LTB. Other studies suggest northern pygmy-owls are scarce above 1,800 m in California (CWHR 2000) whereas flammulated owls have been found up to ~2,900 m (Winter 1974, Shuford and Fitton 1998). Western screech-owls were not detected during my study;

U.S. Forest Service researchers have also rarely detected screech-owls incidentally during surveys for California spotted owls (T. Farnum, personal communication). The lack of western screech-owls detections in the basin indicates this species may be at the apex of its elevational range in the region (Verner and Boss 1980).

Detection probability

The probability of detecting a saw-whet if it was present in the vicinity of a call point was 0.03–0.25 and depended on the number of visits, the number of call points, and the time of year. In the LTB, surveys beginning in March and ending in early June were more effective at detecting saw-whets than surveys that extended from May to July. This is not surprising, given the owl's breeding behavior. Courtship and establishment of territories can begin as early as February (Cannings 1993) and owls respond more readily to the calls of conspecifics during this time (Palmer 1987). Owls continued to respond to broadcast surveys in June and July, but the calls usually consisted of squeaks or chirps rather than the typical advertising call, which made it difficult to identify the species.

Although saw-whets were more abundant than other small owl species, the probability of a saw-whet occupying the vicinity of any given call point was low (0.23). Given the low probabilities of both occupancy and detection, MacKenzie and Royle (2005:1110) suggested an optimum number of 7 visits per call point (i.e., site) in future surveys for saw-whets. Seven visits would result in a low probability of not detecting an individual when it is in fact present (i.e., 0.05–0.15) and allow for the development of reliable inferences regarding occupancy and habitat associations. To decrease survey

effort, however, a removal sampling design could be implemented. With this design, a maximum number of visits is determined and each point is surveyed until a saw-whet is detected or the maximum number of surveys are conducted (MacKenzie and Royle 2005). With a probability of occupancy of 0.23 and probability of detection of 0.25 for saw-whets, MacKenzie and Royle (2005:1112) recommended at most 9 visits per site to maintain a low probability of a false absence. Although the removal design requires a larger initial number of visits per site than the standard design, the idea is that surveyors will need to conduct fewer surveys in total. Fewer visits could be made if researchers are willing to accept a higher probability of a false absence.

I did not calculate detection probabilities for flammulated or northern pygmy-owls due to limited detections of those species. Based on the detections I did acquire, it appeared that initiating surveys in the LTB in March was adequate for northern pygmy-owls but may have been too early for detecting the migratory flammulated owl, whose earliest detection during my study was in mid-May. The diurnal northern pygmy-owls were detected either shortly after sunrise or within 30 minutes of sunset, indicating that attempts at surveying for this species after ~2100 may not be an efficient use of time. Flammulated owls, on the other hand, often called for long periods of time and were never detected prior to ~2100.

Habitat associations

Saw-whet owls are found throughout southern Canada, northeastern and western United States, and western Mexico (Johnsgard 2002:234). They require a mix of open and dense forest for foraging and roosting, respectively, along with adequate nest sites for

reproducing (Johnsgard 2002). Saw-whets occur in a variety of vegetation types, from coniferous stands (Anderson and Clark 2002, Rocky Mountains) to deciduous dominated forests (Dumas 1950, southeast Washington) to mature riparian habitats (Hayward and Garton 1988, Idaho). In the Glass Mountain region, Shuford and Fitton (1998) found 39% of the detected saw-whets in stands of Jeffrey pine, 21% in pinyon pine (*Pinus monophylla*) woodland, 16% in lodgepole forests, 14% in mixed stands of Jeffrey pine, lodgepole pine, or white fir, and 10% in quaking aspen stands or aspen mixed with Jeffrey or lodgepole pines. Their results were similar to my study, although I had a higher proportion of owls detected in areas dominated by red fir (which does not typically occur in the Glass Mountain region).

In the LTB, the saw-whets occurred in a wide range of conditions. At the spatial scales I examined, it appeared that few factors influenced the distribution of saw-whets in the LTB. Of notable interest, however, was that areas dominated by white fir (i.e., west side of the basin) were correlated with the absence of saw-whets at both the macrohabitat and microhabitat scales. The percent of correct predictions was higher for the macrohabitat scale, indicating the correlation may be of greater significance when determining saw-whet distribution at larger spatial scales (i.e., >250 ha). Although white fir exists in higher proportions today than 200 years ago (Manley et al. 2000), there is no indication in the literature as to why white fir itself may influence the presence of saw-whets. Interestingly, in a study of secondary cavity-nesting songbirds in central Sierra Nevada, north of the LTB, Raphael and White (1984:54) concluded that the songbirds preferred white fir snags for nesting. It is possible white fir was merely

acting as a proxy for other factors that I did not measure in my study. For example, Parker (1984, 1986) found white fir, when compared with red fir in the Sierra Nevada, tended to dominate in areas of lower elevations, less steep slopes, more fertile soils, and more closed canopy. These differences in the biotic and abiotic conditions between white and red fir stands could result in different understory vegetation composition which, in turn, could impact small mammal abundance or availability (e.g., Verner and Boss 1980). Small mammals (*Peromyscus* and *Microtus* spp. in particular) are the main prey of saw-whet owls (Cannings 1993) and it may be the abundance or availability of small mammals that influenced saw-whet occurrence rather than the presence of white fir. For example, in the northern Sierra Nevada, Coppeto et al. (2006) found small mammal abundance and diversity were lower in white fir forests than red fir forests, due in part to a dense vegetation layer in the understory of red fir forests.

Given the importance of small mammals in the saw-whet's diet, and the ground-dwelling nature of many small mammals, the extent of open ground may dictate their availability to owls. Although areas of dense shrub cover occurred at high elevations, open ground was also more notable at high elevations (dominated by red fir), where saw-whets typically occurred, than at lower elevations. Thus, the availability of small mammals, rather than abundance alone, may be an issue for the saw-whets in some areas of the basin.

The amount of area within macrohabitat sites covered by the various forested or non-forested vegetation types was similar between use and non-use sites. An extension of this inquiry was the calculation of edge density. Researchers have noted the use of

forest edge or forest openings by the owls for hunting (Forbes and Warner 1974, Cannings 1993, McCallum 1994). I considered edge to be the boundary between forested and non-forested areas, regardless of whether the non-forested areas were shrubland, herbaceous vegetation, sparse vegetation, or barren. Non-forested areas tended to be patches of varying size scattered throughout the basin within the matrix of open or closed canopy forest. Edge density was a measure of the extent of forest fragmentation within each macrohabitat site, with the fragmentation in most sites due to natural causes. Although saw-whets hunt along edge habitat, the amount of edge within a site did not appear to be important. Palmer (1986) and Hayward and Garton (1988) speculated that the high maneuverability of saw-whets, due to the light wing loading of the species, may allow them to hunt with relative ease in areas of heavy cover and limit the need for edge habitat or open areas.

At the microhabitat scale, nearly 60% of the detected saw-whets were on westerly or northerly aspects and 45% were located on slopes of intermediate grade. In general, the aspect of owl locations was likely a result of the bowl-like shape of the basin: most saw-whets were detected in the southern and eastern sections of the basin where the overall aspect tended to be north and west, respectively. In addition, steeper slopes often corresponded with higher elevations. Nearly 2 times as many saw-whets were detected in elevations >2,200 m than in lower elevations, corresponding to the majority of owls that were detected at points of intermediate to steep slopes.

On average, I detected saw-whets further from paved roads than non-use points, although this was not statistically different. The distance from roads was likely due to

the fact that the network of paved, local roads extended further into the watersheds on the west side of the basin, where fewer owls occurred, than in the southeast, where more owls occurred. Females are known to abandon their nest if disturbed early in the breeding season (Cannings 1987), which may occur in areas where vehicle and human access is facilitated by the presence of roads. Locations of winter roosts, however, indicate the owls may survive well in rural or semi-rural areas (Cannings 1993). The effects of current human disturbances (e.g., roads, vehicular traffic, recreation) on saw-whet distribution and behavior require further investigation.

Snag characteristics did not appear to limit or restrict the distribution of saw-whets in the basin. Snags are plentiful in the basin and exceed U.S. Forest Service snag retention guidelines of ~7–15 snags/ha (3–6 snags/acre) (U.S. Forest Service, LTBMU, unpublished guidelines, Hutto 2006); potential nest sites for the owls seem ample. Densities of large snags ≥ 40 cm DBH are at the high end of the USFS guidelines, averaging ~16 per ha. That snag densities were higher in the white-fir dominated western section of the basin could be explained, in part, by the fact that mortality of white fir, along with Jeffrey pine, increased in the early 1990s due to epidemic levels of bark beetles (e.g., the fir engraver beetle [*Scolytus ventralis*] and Jeffrey pine beetle [*Dendroctonus jeffreyi*]) (Rizzo and Maloney 2000). Although snag densities were higher in white-fir dominated areas, where I detected fewer saw-whets, correlating snag densities with owl occurrence may be misguided. There are numerous differences between the western section of the basin and other areas, besides the preponderance of snags and white fir, that may be driving the absence of saw-whets: the microclimate is

wetter, snow remains on the ground later into the year, vehicle access is easier and more frequent, let alone as yet unmeasured variables (e.g., prey abundance and availability). Although snags are abundant in the basin, snags themselves are only one of several components needed for the creation and use of nest sites. Suitable cavities must exist in the snags, the species that create cavities must occur in the area (the number of excavated cavities typically exceeds that of naturally formed cavities [Raphael and White 1984]), and competition from other secondary cavity-nesters – songbirds and owls alike – must not exceed cavity availability. The average of 3–5 cavities/ha in my study area suggested that an adequate cavity density occurred in the basin for saw-whet owls.

Regarding the possible influence of heterospecifics in saw-whet distribution, I detected saw-whets further from the large owls, on average, yet the distance between saw-whets and the large owls was extremely variable, ranging from 30 to nearly 10,000 m. Long-eared, great horned, and spotted owls are known predators of saw-whets (Voous 1989), yet the presence of the large owls appeared to be less important in determining saw-whet distribution than other habitat variables in my study.

My data indicated clustering of saw-whets in the basin. Researchers have noted clustering in other owls species, but information in the literature is lacking with regards to potential clustering of saw-whets. Arsenault (1999) found aggregations of breeding flammulated owls in New Mexico and suggested it may be due to cavity availability. Communal roosting of long-eared owls occurs in the winter (Johnsgard 2002:205). Although reasons for communal roosting are unknown, Bosakowski (1984) speculated it may reduce predation risks. In their study of spotted owl settlement patterns, Seamans

and Gutierrez (2007) found that immigrants tended to settle closer to sites already occupied by spotted owls. Owls new to the area may use the presence of other owls as indications of suitable habitat (Seamans and Gutierrez 2007, Campomizzi et al. 2008). Whether the clustering of saw-whets in the LTB was related to availability of resources or due to some social component (conspecific attraction) of the species is not discernible with my study. Measuring clustering of individuals was a simple, preliminary examination and was not designed to differentiate the mechanisms behind the event. It nevertheless warrants further investigation, especially with its potential as being an important factor in developing our ability to predict owl occurrence.

Although I detected few flammulated and northern pygmy-owls, my results implied the distribution of flammulated owls may be more restricted than either saw-whets or northern pygmy-owls in the basin. The 5 flammulated owls occurred in relatively open, west-facing slopes from which snow melted early in the spring. Three of the individuals occurred at sites with a relatively high proportion of quaking aspen snags. Aspen stands are typically found in mesic areas adjacent to shrub or meadow habitats and, thus, tend to have higher insect production (Mayer and Laudenslayer 1988). These areas likely provide better foraging opportunities for the insectivorous flammulated owl (McCallum 1994). Northern pygmy-owls, however, feed on a wide variety of prey (Holt and Petersen 2000) and may be somewhat less constrained in distribution in the basin. Songbirds are an important prey item for northern pygmy-owls, and since cavity-nesting songbirds tend to prefer white fir snags for nesting (Raphael and White 1984), prey availability could be driving the occurrence of pygmy-owls in the

western side of the basin. Given the apparent rarity of flammulated owls and northen pygmy-owls in the basin, future research and analyses of habitat associations of these species may need to extend beyond the basin boundaries to obtain adequate sample sizes.

One limitation of my study is that I quantified habitat characteristics of owl activity areas based on their responses to nocturnal broadcast surveys; the presence or absence of owls in certain areas, while indicative of activity, does not speak directly to the quality of the habitat (e.g., Van Horne 1983). Locating owl nests and determining reproductive success – information more appropriate for assessing habitat quality – required time and effort that was infeasible for my study. Thus, habitat quality of the areas in which owl were or were not detected cannot be known directly. However, the detection of 3 juvenile saw-whets in the vicinity of 3 different microhabitat sites did indicate suitable breeding habitat in those areas. Examining the reproductive success of saw-whets throughout the basin, rather than focusing solely on occurrence, would provide a necessary measure of habitat quality.

SUMMARY OF MANAGEMENT IMPLICATIONS

While it appears that the needs of northern saw-whet owls are being met in the LTB, high snag densities and a high relative abundance of white fir, compared with 200 years ago, serves to emphasize the need for restoration in the basin. Land managers are well aware of the need for restoration in the Sierra Nevada and numerous restoration projects are currently underway to decrease snag densities and return tree species composition to a state more similar to that of pre-European settlement (e.g., LTBMU 2008). It is difficult to assess how many snags are a sufficient amount in a forest, and the number is certainly influenced by surrounding conditions and circumstances (e.g., proximity to human development). Nevertheless, the U.S. Forest Service snag retention guidelines recommend retaining ~7–15 snags/ha (3–6 snags/acre), depending on vegetation type (U.S. Forest Service, LTBMU, unpublished guidelines, Hutto 2006). All sites combined, the average snag density was ~3 times greater than the highest recommended density. It appears that removing some snags, especially those of smaller diameter, would not negatively impacts the saw-whet owls in the LTB.

Restoration would result in a shift of some habitat variables. The effects of habitat changes on the populations of small, cavity-nesting owls in the LTB are, as yet, unknown. Thus, monitoring of the small owls is an essential component for management of the species. Monitoring will indicate whether changes that occur with the populations of interest are due to management activities, and whether those changes are proceeding in the desired direction (Morrison et al. 2008:267). The results of my

study can aid in developing a monitoring protocol. For example, nocturnal surveys for saw-whets and crepuscular surveys for northern pygmy-owls should occur between March and June, whereas nocturnal surveys for flammulated owls should begin in early May. Call points should be spaced at least 500 m apart and visited 7 times for an acceptable probability of a false absence. In addition to monitoring, future studies on the reproductive success of saw-whets would help define the factors that enable the persistence of healthy populations of saw-whets in the Sierra Nevada and aid in directing restoration efforts.

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